ROBUSTNESS AND HIERARCHICAL CONTROL OF PERFORMANCE VARIABLES THROUGH COORDINATION DURING HUMAN LOCOMOTION

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ROBUSTNESS AND HIERARCHICAL CONTROL OF PERFORMANCE VARIABLES THROUGH COORDINATION DURING HUMAN LOCOMOTION

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LIST OF TERMS AND ABBREVIATIONS

Local Variables	Smallest, most numerous time-dependent elements within a defined system whose characteristics are based on anatomical or physiological organization. For this dissertation work, these are segment angles
Leg vector	A line whose endpoints are defined by the toe and pelvic ASIS markers in the sagittal plane that contains information about both magnitude and direction.
Leg length	Magnitude of the leg vector
Leg orientation	Angle of the leg vector relative to horizontal
Performance Variable	Higher level element within a system's hierarchy whose characteristics are defined by task function, rather than by strict anatomical or physiological organization. For this dissertation work, this is leg length or leg orientation.
GEV	Goal Equivalent Variance: Local variable variance that does not change the performance variable
NGEV	Non-Goal Equivalent Variance: Local variable variance that does change the performance variable
IMA	Index of Motor Abundance: Metric of normalized difference between GEV and NGEV
Stabilization	The minimization of cycle to cycle variance of the performance variable (leg length or leg orientation)
Variance Structure	Partitioning of the variance of local variables into GEV and NGEV components
UCM	Uncontrolled Manifold: An operational subspace that contains the set of all local variable combinations that achieve the same, desired value of the performance variable
Operational space	Used synonymously to describe the UCM or set of solutions that are available to achieve the desired performance variable

SUMMARY

The kinematic motor redundancy of the human legs provides more local degrees of freedom than are necessary to achieve low degree of freedom performance variables like leg length and orientation. The purpose of this dissertation is to investigate how the neuromuscular skeletal system simplifies control of a kinematically redundant system to achieve stable locomotion under different conditions. I propose that the neuromuscular skeletal system is focused on minimizing step to step variance in leg length and orientation while allowing segment angles to vary within the set of acceptable combinations of angles that achieves the desired leg length and orientation. I first determine whether control of the locomotor system is organized hierarchically such that leg length and orientation are achieved through interjoint compensation by structuring segment angle variance. This will be studied in the context of human hopping, a locomotion model that has been well studied and the dynamics of which can be modeled using a simple spring-mass model. I further test the robustness of compensation strategies under different hopping conditions and perturbations, including frequency, constrained foot placement, and different speeds. The results of this study will give valuable information on interjoint compensation strategies used when the locomotor system is perturbed. This work also provides evidence for neuromuscular system strategies in adapting to novel, difficult tasks. This information can be extended to give insight into new and different areas to focus on during gait rehabilitation of humans suffering from motor control deficits in gait.

CHAPTER 1

INTRODUCTION

Locomotion is a consistent, cyclical task that is performed on a daily basis. Locomotion is the result of the complex interplay between many different elements of the human body. Interactions with the environment require constant integration of sensory feedback and coordination of the lower limbs to cope with unexpected perturbations. How control of such a complex system is achieved is one of the most difficult questions to answer in motor control research.

The purpose of this dissertation work is to gain insight into how the neuromuscular skeletal system controls the human body to achieve stable locomotion even when presented with task constraints. I will show that the neuromuscular skeletal system uses kinematic motor redundancy to minimize cycle to cycle variations of task-level kinematic performance variables that are critical for completing a gait cycle. I will show evidence that during human hopping, leg length and leg orientation are task-level performance variables whose variance is minimized depending on timing in the cycle and task demands.

1.1 Motor Redundancy

Kinematic motor redundancy was first described by Bernstein when he observed that to reach any point in space, there were an infinite number of joint combinations and trajectories that would result in the hand reaching the same place (Bernstein 1967). This is true because to reach any point in 3D space, only six degrees of freedom are required and the human body has many more degrees of freedom at its disposal. In other words,

the human body is redundant. The significance and role of the neuromuscular system's motor redundancy, or "motor abundance" in more recent works (Latash 2000), has been well studied in upper extremity tasks (Latash et al. 2001; Latash et al. 2002b; Scholz and Schöner 1999; Tseng et al. 2002; Tseng and Scholz 2005; Tseng et al. 2003), sit to stand (Scholz et al. 2001), and postural control (Krishnamoorthy et al. 2004; 2003; McKay and Ting 2008; Scholz et al. 2007; Ting 2007; Ting and McKay 2007). The results of these studies suggest that motor redundancy is used to achieve repeatable overall task performance. Despite evidence for motor redundancy being used in all these tasks, there is little research exploring the use of motor redundancy in locomotion.

The locomotor system of the human body has redundant kinematic degrees of freedom. In the sagittal plane, placement of the foot anywhere only requires two degrees of freedom yet there are three major joints, the ankle, knee and hip. Locomotion is an ideal task in which to study cycle to cycle variations in task performance because unlike most other tasks that have been previously studied, movement of the lower limbs is truly a cyclical task in everyday life. From cycle to cycle, locomotion appears very stable and consistent. What may not be evident is the locomotor system's constant compensation to perturbations. These perturbations can be encountered acutely, for example, when stepping onto softer or harder surfaces (Ferris and Farley 1997; Ferris et al. 1999; Ferris et al. 1996; 1998; Moritz and Farley 2003; 2005; 2004). Or, perturbations can be chronic, as in the case of gait pathologies due to neurological impairments such as hemiparetic stroke or Down syndrome (Black et al. 2007; Perry et al. 1995; Wagenaar and Beek 1992) or assistive and resistive joint loads (Chang et al. 2008; Ferris et al. 2006).

Regardless of the type of perturbation, the locomotor system is able to quickly respond and make compensatory adjustments to achieve stable locomotion.

Whether from step-to-step or over the course of days or months, I predict that kinematic motor redundancy is exploited to maximize our ability for perturbation compensation. I propose that the inherent lower limb kinematic motor redundancy is organized to compensate for perturbations to achieve functional outputs or task critical performance variables.

1.2 Hierarchical organization

The human motor control system is a very complex system. Movement is the concerted output of many different elements at many different levels of the neuromuscular system. Control of all these elements seems like a daunting task, especially when we consider the possibility that each element or degree of freedom could be controlled independently. There is evidence that suggests this control is simplified through hierarchical organization of these elements into different levels. Because examples of hierarchical organization exist at several different levels of the neuromuscular system, it would appear this organization may be a robust strategy by which the human body manages its many different elements. In this section, I will discuss some examples of hierarchical organization at different levels physiology for motor control.

The first hierarchical organizations that will be discussed are central pattern generators (CPGs). CPGs are a widely accepted concept and believed to reside within lumbar region of the spinal cord. CPGs are thought to be a group of neurons that are capable of creating rhythmic movements by alternating excitation of many flexor and

extensor motorneurons during locomotion (Brown 1914; Rossignol et al. 2006). Because of the alternating control of flexors and extensors, this CPG model is also referred to as a "half-center" model. A half-center CPG can be described as having two groups of rhythm generation interneurons (half-centers) that project onto either flexor or extensor motorneurons. Pharmacologically induced locomotion using dihydroxyphenylalanine (DOPA) showed interneuron pathways that resulted in alternating excitation of flexor and extensor motorneurons (Jankowska et al. 1967). Since the idea of CPGs was first conceived, this simplistic model has been expanded to include multiple organizational levels to account for more complex patterns. One proposal of this is a two-level half-center CPG model where the rhythm and pattern generators are distinctly separated (McCrea and Rybak 2008; Rybak et al. 2006a; Rybak et al. 2006b). In this model, there is hierarchical control of rhythm and pattern generating interneurons that then project onto many flexor or extensor motorneurons. CPGs are an example of hierarchical organization in locomotion. Control of a large number of muscles is achieved organizing these muscles into flexors or extensors and providing rhythm and pattern formation information to achieve locomotion.

Another level of motor control that shows hierarchical organization is at the muscle level. This organization is studied in the context of muscle synergies. A muscle synergy is a pattern of muscle activations from a recorded set of muscles. When combinations of different muscle synergies are activated, these combinations are found to correlate with a wide range of postural tasks (Macpherson 1991; 1988; Ting 2007; Torres-Oviedo et al. 2006). Force vectors necessary to achieve stable posture are the products of muscle forces. In a simulation model, as few as five muscle synergies have

been shown to be able to reproduce force vectors observed when perturbing the posture of cats (McKay and Ting 2008). The existence of similar muscle synergies have also been shown in locomotion (Tresch et al. 1999; Tresch et al. 2002)and human postural control (Krishnamoorthy et al. 2004; 2003; Ting 2007; Ting and McKay 2007). While the relative patterns of muscle activations seen within a muscle synergy do not change between tasks, the absolute magnitudes of muscle activations within a synergy can change with tasks. It has been suggested that the magnitude of muscle activation or gain within a muscle synergy is controlled through a single neural command signal for different tasks (Ting and McKay 2007). The combination of different muscle synergies and magnitude gains provide a robust model to simplify control of a very complex system of muscles to achieve different tasks.

The highest level of hierarchy to be discussed is at the joint and task level. The motor redundancy of joint level variables is organized to achieve higher order, task level performance variables during reaching, force production, posture, and sit to stand tasks (Desmurget et al. 1995; Domkin et al. 2002; Latash et al. 2001; Latash et al. 2002b; Loeb et al. 1999; Scholz et al. 2001; Scholz and Schöner 1999; Scholz et al. 2007; Shinohara et al. 2003a; Shinohara et al. 2003b; Ting and McKay 2007; Todorov et al. 2005; Tseng et al. 2002; Tseng and Scholz 2005; Tseng et al. 2003; Yang et al. 2007). Examples of hypothesized performance variables in these studies include endpoint position of a finger, total force production by fingers, and body center of mass position. Joint and task level variables include joint kinematics or finger forces. All these studies have shown that the variance of task level performance variables are minimized, or stabilized, through coordination of joint level variables. These task level performance variables can be

described as existing at a higher hierarchical level than muscle synergies. This level of hierarchical control contains a set of variables that have been referred to as "functional synergies" (Latash et al. 2002b). While the term "synergy" is used to describe both the muscle level described previously and this functional level, it is important to understand how this term is used in the context of both levels, specifically in regards to regulation of local variables. In the context of muscle synergies, the local variables are the muscle activations and the synergy is the pattern of muscle activations that are recorded in response to a task. In the context of functional synergies at higher hierarchical levels, a term "synergy" is used to describe a covariation of local variables that act to stabilize a higher order performance variable. This covariation is quantified by analyzing the variance structure of local variables. However, how control and covariation of local variables operate within a functional synergy is not as clear as the control of muscles within a muscle synergy. This organization also allows for flexible regulation of redundant joint level variable and control of fewer performance level variables at each higher level of the hierarchy. It is this hierarchical organization of joint variables and performance variables that this I will explore.

Hierarchical organization of performance variables during locomotion is less researched. However, there is evidence to suggest that there is dimensional reduction of control during locomotion. When three dimensional movements of the foot, shank, and thigh segment angles are plotted against each other in 3-D space for a variety of gaits, including hopping, the resulting data collapse onto a simple plane (Borghese et al. 1996; Grasso et al. 2000; Ivanenko et al. 2007; Ivanenko et al. 2008). Yet, the reason the neuromuscular system operates in a two dimensional plane when it has a three

dimensional space at its disposal is not clear. The first aim of this dissertation is to identify whether there is purposeful organization of joint level variables to stabilize higher order limb level performance variables during locomotion. This will be done through an analysis of variance of hypothesized joint level and task level performance variables during locomotion.

1.3 Redundancy exploited within an "Uncontrolled Manifold"

Using variance as a metric for testing hypotheses about movement control is well established in the motor control literature (Latash et al. 2001; Latash et al. 2002b; Scholz et al. 2001; Scholz and Schöner 1999; Scholz et al. 2007; Scholz et al. 2000; Tseng et al. 2002; Tseng and Scholz 2005; Tseng et al. 2003). A method for analyzing whether cycle to cycle deviations of performance variables are minimized or stabilized through the structuring of local joint variance was introduced by Scholz and Schöner (Scholz and Schöner 1999). This method is based on the Uncontrolled Manifold hypothesis which states that joint variance is "structured" or restricted by the nervous system only if the variance results in deviations away from a desired performance variable. Joint variance that does not result in deviations away from a desired performance variable is permitted within an 'Uncontrolled Manifold' (UCM). The UCM analysis is a computational method that calculates the UCM through a linearized model and quantitatively relates variance in joint level variables (e.g. segment angles) to small changes in performance variables (e.g. leg length or orientation). The linearized model of the UCM analysis allows us to see how variance at the joint level is partitioned for the stability of the performance variable. Because the UCM is a linear space, variance can be partitioned into components that are parallel and orthogonal to the UCM. The parallel component of variance allows for

different joint level variable combinations that do not change the desired performance variable. The orthogonal component of variance is joint level variable combinations that results in changes to the desired performance variable. This quantifiable structure of joint level variance allows us to test whether functional synergies exist. More specifically, we can test whether a stabilization strategy exist where the variance of joint level variable inputs are purposefully structured to achieve performance variable output.

Many studies have tested the existence of functional synergies within the framework of the UCM hypothesis. Most of these studies have involved upper extremity tasks (Latash et al. 2002a; 2001; Latash et al. 2002b; Scholz et al. 2001; Scholz and Schöner 1999; Shinohara et al. 2004; Tseng et al. 2002; Tseng and Scholz 2005; Tseng et al. 2003) with few investigating the role of neuromechanical redundancy in the control of the lower extremities during human locomotion (Black et al. 2007; Robert et al. 2009). Using a UCM analysis, I will identify stabilization strategies in human hopping. Hopping, a bouncing gait, was selected because the dynamics of bouncing gaits can be modeled as a simple spring-mass model which may give insight into potential task level performance variables.

1.4 Spring-mass model for bouncing gaits and performance variables

The choice of human hopping as my locomotion model is critical because the dynamics of bouncing gaits have been well studied and can be approximated by a simple, low degree of freedom spring-mass model (Chang et al. 2008; Farley et al. 1987; Farley et al. 1991; Farley et al. 1985; Farley et al. 1998; Farley and Morgenroth 1999; Ferris et al. 2006; Ferris and Farley 1997). Simple yet robust models of gait like the spring-mass model have the advantage of focusing on how different physiological factors in the

locomotor system act in concert to achieve whole system functional outputs and limb level task goals. Based on the spring-mass model, the limb level goals of hopping are limited to only a few potential task-level performance variables: leg length, leg orientation, end-point force, and stiffness. As discussed in the previous section, the human locomotor system is kinematically redundant. In the sagittal plane, the human lower limbs can be characterized by four segment angles. Together, these four segment angles make the largest contributions to the overall flexion and extension of the legs. From the potential task-level variables of the spring-mass model, leg length and leg orientation are kinematic variables that may be stabilized to achieve the stable spring-mass dynamics observed.

In addition to classic biomechanics research that support leg length and orientation as possible performance variables, recent neurophysiological studies provide further evidence of a neural representation for kinematic elements of the spring-mass model. These studies showed that whole limb geometry (leg length and orientation) was represented in specific populations of neurons within the central nervous system at the level of the spinal cord (Bosco and Poppele 2003; 2000; Bosco et al. 2000; Poppele et al. 2002). The first aim of my dissertation will be to ascertain whether segment angle variance is purposefully structured to stabilize the performance variables leg length or leg orientation from cycle to cycle errors (**Chapter 2**).

1.5 Effect of tasks constraints

The second aim of my dissertation is to determine the robustness in the structuring of segment angle variance to stabilize leg length or leg orientation across different hopping conditions. Since different combinations of muscle synergies can

produce a variety of tasks, leg length and leg orientation stabilization strategies might also be robust across a variety of task conditions. Little work has been done to explore how performance variable stabilization strategies vary across different task conditions and even less in the context of locomotion. A recent study involving children with Down syndrome (DS) observed more joint-level variance was structured for the purpose of stabilizing center of mass position when compared to typically developing children (Black et al. 2007). Through a UCM analysis, they suggest that the increased joint angle variance due to the inherently unstable mechanics of children with DS required that variance to be structured to achieve center of mass stabilization. This study revealed differences in center of mass stabilization strategies of typically and atypically developed children during locomotion. However, this study reveals little in terms of how a stabilization strategy is modulated within an individual as task conditions change.

While no study has quantified how stabilization strategies change with different locomotion constraints, some studies have shown changes in stabilization strategies with constraints on other tasks. These studies were done using a UCM analysis to quantify whether changes in joint level variance is structured toward the stabilization of hypothesized performance variables as the task constraints increased the task difficulty. In an early study using the UCM analysis, a sit-to-stand task was studied (Reisman et al. 2002a; Scholz et al. 2001; Scholz and Schöner 1999). These authors hypothesized that the center of mass or the position of the head might be task critical performance variables that would be stabilized by structuring the variance of trunk and leg joint angles. They also hypothesized that decreasing the base of support width would increase the total variance of the joints. The results showed that increased variance was structured into the

UCM to stabilize the center of mass or the position of the head. Similar results were seen in other tasks where task difficulty was manipulated. In an upper extremity task such as moving a finger to a target area, removing vision resulted in increased total variance of upper limb joints. (Tseng et al. 2002; Tseng et al. 2003). Repeating the task in the non-dominant hand showed even higher increases in variance of the arm's joints. In both cases, the increased variance was structured into the UCM to stabilize the endpoint position of the hand. Similar results have been shown for finger force production tasks (Latash et al. 2001). The increase in joint level variance in response to a variety of task constraints and task difficulties appear to be consistently structured toward stabilizing performance variables.

Different perturbations during human locomotion can place additional constraints on locomotion. Some constraints can even increase the overall difficulty of locomotion. To test whether increased difficulty requires increased structuring of segment angle variance to stabilize leg length or orientation during locomotion and the robustness of the response, I will use three locomotion constraints that will affect different performance variables. First, I will ask subjects to hop in place at non-preferred frequencies (**Chapter 2**). Second, I will ask subjects to hop in place into a target area that limits their landing area (**Chapter 3**). Each of these constraints was chosen to increase the difficulty of different performance variables during human hopping, the rationale and specifics of which will be discussed in respective subsequent chapters. By choosing two different task constraints, I can test the robustness of the leg length or leg orientation stabilization strategies across hopping in place conditions. I can also test whether there is a predictable change in leg length or leg orientations stabilization strategies due to changes in task

constraints and difficulty. My third perturbation was to apply two simultaneous task constraints by asking the subjects to hop forward at 0.8 m/s into a target area that limits their landing area (**Chapter 4**). This dual constraint serves two purposes. First, as traditional locomotion typically has a forward component, the forward velocity component will show whether the leg length and orientation stabilization characteristics observed during hopping in place translate to forward locomotion. Second, because the response of leg length and leg orientation to changes in landing target area is quantified during hopping in place (**Chapter 3**), any changes seen in leg length or leg orientation stabilization at different target sizes during forward hopping will be due solely to the forward velocity component.

1.6 Aims and objectives

The aim of this dissertation is to explore how kinematic motor redundancy of the neuromuscular skeletal system is hierarchically organized to stabilize task critical kinematic performance variables during locomotion. I hypothesize that the inter-cycle variance of lower limb segment angle trajectories is structured to stabilize leg length or leg orientation from cycle to cycle errors during locomotion. This will be explored within the framework of a UCM analysis and human hopping (**Chapter 2**). I also hypothesize that as task constraints cause the task difficulty to increase, more segment angle variance must be structured to stabilize leg length or leg orientation when they are critical to task completion. Task constraints will include 1) hopping at non-preferred frequencies (**Chapter 2**) and 2) hopping into different size target areas (**Chapter 3**). Finally, I will test the robustness of leg length and leg orientation stabilization strategies in forward locomotion with different size target areas to test whether previously observed strategies

translate to forward locomotion (**Chapter 4**).

CHAPTER 2

DESCRIPTION OF LEG LENGTH AND LEG ORIENTATION RELATIONSHIP WITH SEGMENT ANGLES DURING HUMAN HOPPING AT PREFERRED AND NON-PREFERRED FREQUENCIES

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2.1 Introduction

The human locomotor system is equipped with more degrees of freedom than is necessary to execute a locomotion task. The dynamics of bouncing gaits can be approximated by low degree of freedom spring-mass models that simplify global kinematic function of the leg into two performance variables: length and orientation. Yet, in the sagittal plane, there are three major joints of the leg that contribute significant amounts of flexion and extension to determine overall leg length and leg orientation. This is an example of kinematic motor redundancy, a phenomenon first reported by Bernstein. He observed that neuromechanical redundancy during limb control allowed for the accomplishment of a desired goal in a kinematic task through a number of different possible trajectories (Bernstein 1967). The classic motor control problem addresses exactly how the neuromechanical system chooses to achieve control of a task level performance variable.

Whether from cycle to cycle or over the course of days and months, I predicted that the human locomotor system exploits neuromechanical redundancy to maximize adaptability to perturbations. These perturbations can be encountered acutely, for example, when stepping onto softer or harder surfaces (Ferris and Farley 1997; Ferris et al. 1999; Ferris et al. 1996; 1998; Moritz and Farley 2003; 2005; 2004). Or, perturbations can be more chronic, as in the case of chronic gait pathologies due to neurological impairments such as hemiparetic stroke (Black et al. 2007; Perry et al. 1995; Wagenaar and Beek 1992). In both types of perturbations, the locomotor system must make compensatory adjustments to achieve stable locomotion. I proposed that the inherent neuromechanical redundancy within the legs is exploited during human locomotion to stabilize key performance variables against cycle-to-cycle perturbations.

In addition to classic biomechanics research that supports leg length and orientation as low degree of freedom performance variables, recent neurophysiological studies provide further evidence of a neural representation for kinematic elements of the spring-mass model. These studies showed that whole limb geometry (leg length and orientation) was represented in specific populations of neurons within the central nervous system at the level of the spinal cord (Bosco and Poppele 2003; 2000; Bosco et al. 2000). Yet, little insight has been gained into how these performance variables are achieved by the nervous system. Given that there exists an abundance of possible joint angle combinations for any whole limb geometry (leg length and orientation), control of this kinematically redundant locomotor system might involve independent control of each joint. Alternatively, the most parsimonious solution requires a reduction of control parameters in the lower limbs that utilizes the locomotor system's inherent motor

abundance. Although much is known about the whole body biomechanics of human hopping, a fundamental question that remains unanswered is whether there is an actual physiological mechanism in the nervous system that references a neuromechanical representation of the spring-mass system during locomotion. As a first step, I investigated whether higher-level kinematics associated with spring-mass dynamics like leg length and orientation observed during bouncing gaits were stabilized by interjoint compensation.

Studies using non-linear dynamics approaches often define stability as the tendency of a task variable to return to a limit cycle. This is often measured in theoretical mechanics using techniques such as Lyapunov exponents or Floquet multiplers. These approaches have sometimes shown that task variance does not correlate with the dynamic stability of the task variable to return to its limit cycle (Dingwell et al. 2001; Dingwell and Kang 2007; Dingwell and Marin 2006; Dingwell et al. 2008). Still, others have regarded the minimization of variance to be an important feature of skilled performance (John and Cusumano 2007), particularly if it conveys information regarding the functional relationship between body-level variability and goal-level variability (Cusumano and Cesari 2006). In the present study, I will define "stabilization" as the minimization of task-level variance (i.e. leg length and orientation) through the purposeful structuring of segment angle variance. Furthermore, I make an operational assumption that task stability through joint-level variance structure is related to the neuromechanical control of the task variable, which may have contributions from both active neural and passive mechanical processes. My definition of "stability" is consistent with the body of research involving the UCM approach (Scholz and Schöner 1999;

Scholz et al. 2007; Tseng et al. 2002; Tseng and Scholz 2005; Tseng et al. 2003) and with others that employ the dynamical systems approach (Kelso 1994; Schoner and Kelso 1988).

Using kinematic variance as a metric for testing ideas about movement control is well established in the motor control literature (Latash et al. 2001; Latash et al. 2002b; Scholz et al. 2001; Scholz and Schöner 1999; Scholz et al. 2007; Scholz et al. 2000; Todorov and Jordan 2002; Tseng et al. 2002; Tseng and Scholz 2005; Tseng et al. 2003). A method for analyzing the stabilization of performance variables through the coordinated structuring of local variance was introduced by Scholz and Schöner (Scholz and Schöner 1999). Their method is based on the hypothesis that local joint variance is restricted by the nervous system only if the variance results in deviations of the performance variable. Joint variance that does not affect the task is permitted within the 'Uncontrolled Manifold' (UCM), a subset of the joint angle space that is goal-equivalent for the task. The UCM analysis tests this hypothesis by using a linearized model to quantitatively approximate small changes in specific local variables (e.g., segment angles) to small changes in a hypothesized performance variable (e.g., leg length and orientation). The UCM analysis reveals how variance in local joint-level variables is structured to maximize stability of a limb-level variable. This purposeful structuring suggests that joint-level variance acts as a compensation strategy involving interjoint coordination to achieve limb-level stability.

Almost all studies using the UCM analysis involved the study of the upper extremity (Black et al. 2007; Latash et al. 2002a; 2001; Latash et al. 2002b; Reisman et al. 2002a; Scholz et al. 2001; Scholz and Schöner 1999; Scholz et al. 2007; Shinohara et

al. 2004; Tseng et al. 2002; Tseng and Scholz 2005; Tseng et al. 2003). Little consideration has been given to the role of kinematic motor redundancy in the control of the lower extremities during human locomotion (Black et al. 2007; Ivanenko et al. 2007; Reisman et al. 2002a; Scholz et al. 2001; Scholz et al. 2007). There are even fewer studies that have employed the UCM analysis to study the role of motor redundancy in the context of the behaviorally cyclic task of locomotion (Black et al. 2007). There is, however, evidence supporting the idea of dimensional reduction of local variable joint space in human locomotion. The three-dimensional joint angle space created by the thigh, shank, and foot segment angle trajectories are constrained to move within a two-dimensional plane for a variety of gaits (Grasso et al. 2000; Lacquaniti et al. 1990a). More recent studies have shown strong correlations between the observed dimensional reduction and mean whole limb geometry (Ivanenko et al. 2007). It is not well understood, however, what mechanisms are responsible for coordinating this dimensional collapse and to what functional end this mechanism is employed to stabilize for cycle to cycle deviations.

At present, even less is known about how the nervous system exploits neuromechanical redundancy differently when presented with a more constrained, destabilizing system. A few studies have used a UCM analysis to investigate what effects increasing the difficulty of a task have on the stabilization of a performance variable (Reisman et al. 2002a; Scholz et al. 2001; Scholz and Schöner 1999; Scholz et al. 2007). These studies investigated this in a sit-to-stand task repeated over many cycles. Yet, the task of sit-to-stand is a behaviorally discreet task. In contrast, locomotion is a behaviorally cyclic task, making it an excellent model by which to investigate

performance variable stabilization through the use of the UCM analysis. A recent study involving children with Down syndrome (DS) observed these children to structure the increased joint variance more towards stabilizing center of mass position when compared to normally developing children during walking (Black et al. 2007). They suggested that the inherently unstable mechanics of children with DS required utilization of increased interjoint coordination to achieve center of mass stabilization. To test the effects of mechanical stability on the control of well known performance variables (leg length and orientation) during locomotion in a controlled experiment, I increased task difficulty for my subjects by asking them to hop at non-preferred frequencies. A mechanical spring-mass system has a natural resonant frequency dictated by the stiffness of the spring and the mass of the load. When such a system is forced to operate outside of its resonant frequency, the system will always try to equilibrate back to its stable state at the natural resonant frequency. In human bouncing gaits, the resonant frequency, i.e. the frequency at which maximum efficiency and minimum energy expenditure is observed, was found to coincide with a subject's preferred hopping frequency, approximately 2.2 Hz (Cavagna et al. 1997; Farley et al. 1991; Ferris et al. 2006; Holt et al. 1995). When hopping at non-resonant frequencies, subjects likely hop with sub-optimal efficiency and energy expenditure due to an increased demand on the muscles to maintain the hopping frequency. Consequently, a more difficult task is created.

The purpose of this study is two-fold. First, I investigated human hopping within the framework of the UCM hypothesis to study whether a coordinated interjoint compensation strategy is used to stabilize leg length and leg orientation. Second, I tested to see whether the interjoint compensatory strategy changed as I increased the difficulty

of the task by having my subjects hop at frequencies higher than the preferred hopping frequency of 2.2 Hz. I hypothesized that subjects would stabilize both leg length and leg orientation over the entire hopping cycle by coordinating local joint kinematics. They would do this by maximizing the trial-to-trial joint angle variance that lies within the UCM. Furthermore, I hypothesized that there would be increased stabilization of leg length and orientation as I increased the difficulty of the task.

2.2 Methods

2.2.1 Subjects

Eleven healthy human subjects with no prior history of lower extremity injuries volunteered for the study (5 males, 6 females, mean (SD) age = 25(4) yrs, mass = 63.7(10.8) kg). All subjects gave informed consent prior to participating in this study as approved by the Georgia Institute of Technology's Institutional Review Board.

2.2.2 Experimental Protocol

I made anatomical measurements and placed sixteen retroreflective markers on anatomical landmarks of the lower extremities (anterior superior iliac spine, posterior superior iliac spine, thigh segment, lateral femoral epicondyle, shank segment, lateral malleolus, head of the second metatarsal phalangeal joint, and calcaneus). Subjects hopped for three trials at each of three frequencies (2.2, 2.8, and 3.2 Hz) for a total of nine trials. The order of the prescribed hopping frequency was randomized for each subject. Subjects matched their hopping frequency to the beat of a metronome and were given as much time as necessary to practice hopping at the prescribed frequency. Prior to beginning each trial, I visually determined that each subject appeared to consistently

match the prescribed frequency. Each trial lasted approximately thirty seconds. Each subject stood in the center of the force platform, crossed their arms over their chest and hopped on their right leg. After data were collected, only hops within ±3% of the desired hopping frequency were included in my analysis. In most cases, approximately 170 hops were analyzed per subject from each trial.

2.2.3 Kinematics

I used a six camera motion-analysis system (120 Hz; Vicon Motion Systems; Los Angeles, CA) to determine the sagittal plane positions of the ankle, knee, and hip joint centers. I filtered these data using a zero phase shift fourth-order Butterworth low-pass filter with a 10 Hz cut-off frequency. I calculated four segment angles (foot, shank, thigh, pelvis) with respect to horizontal with software coded in Matlab (Mathworks, Natick, MA) using the calculated joint centers along with the toe and the anterior superior iliac spine marker positions and created a linked segment kinematic model (Figure 2.1A). I determined ground contact and liftoff events using a force platform (1080 Hz; AMTI; Watertown, MA) by detecting when the vertical ground reaction force crossed a threshold of 32 N.

Segment angle displacement was defined as the difference in segment angle at touchdown, i.e. initial contact, and the segment angle during maximum leg flexion, i.e. mid-stance (Table 2.1). Leg orientation range was defined as the difference between the maximum and minimum angle of the leg vector relative to the ground during the contact phase.

Table 2.1 Kinematic and stride parameters. Ensemble means (SD) of kinematics and cycle parameters measured. * Significantly different than 2.2 Hz ($p<0.05$). † Significantly different than 2.8 Hz ($p<0.05$)

	2.2 Hz	2.8 Hz	3.2 Hz
Foot Segment Angle at Touchdown, °	148.43 (4.81)	149.39 (5.21)	147.86 (5.17)
Foot Segment Displacement, °	11.62 (2.48)	10.88 (3.08)	12.19 (3.06)
Shank Segment Angle at Touchdown, °	70.59 (1.71)	68.36 (2.00)	67.03 (2.76) *
Shank Segment Displacement, °	-14.34 (1.64)	-5.63 (2.35) *	-2.64 (1.71) * †
Thigh Segment Angle at Touchdown, °	92.50 (1.65)	94.02 (3.16)	96.14 (4.18) *
Thigh Segment Displacement, °	7.55 (2.27)	1.87 (1.67) *	0.49 (0.50) *
Pelvis Segment Angle at Touchdown, °	48.82 (5.11)	49.83 (3.13)	47.84 (5.69)
Pelvis Segment Displacement, °	-1.45 (1.03)	-1.34 (0.98)	-1.13 (1.37)
Leg Length at Touchdown, m	0.93 (0.07)	0.92 (0.06)	0.91 (0.06)
Leg Length Displacement, m	-0.08 (<0.01)	-0.04 (<0.01) *	-0.03 (<0.01) * †
Leg Orientation at Touchdown, °	89.50 (2.59)	89.05 (0.94)	89.10 (0.98)
Leg Orientation Range, °	1.86 (1.34)	1.30 (0.48)	1.45 (0.50)
Measured Hopping Frequency, Hz	2.21 (<0.01)	2.82 (<0.01) *	3.18 (0.05) * †
Hopping Cycle Time, sec	0.45 (<0.01)	0.35 (<0.01) *	0.31 (0.01) * †
Contact Time, sec	0.32 (0.02)	0.26 (0.01) *	0.24 (0.01) * †

2.2.4 Uncontrolled Manifold Analysis

I first defined a leg vector from the toe marker to the anterior superior iliac spine marker as a function of leg segment angles (Figure 2.1). I then created two mathematical functions that related the leg segment angles to either leg length or orientation and linearized them to create two Jacobian models. The first model related changes in the magnitude of this leg vector to changes in the local segment angles. The second model related changes in the orientation of the leg vector to changes in local segment angles.

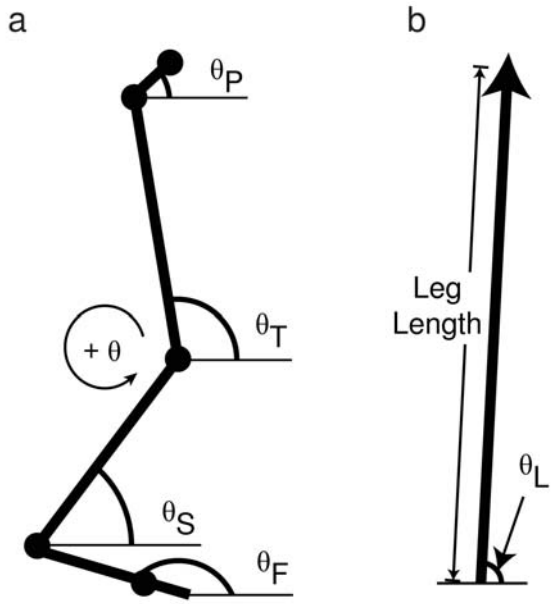

Figure 2.1 : Kinematic Models
(a) Linked segment model that represents the high degree of freedom lower limb with local variables consisting of 4 segment angles: pelvis (θ_P), thigh (θ_T), shank (θ_S), and foot (θ_F); and **(b)** global kinematic variables predicted by the low degree of freedom spring mass model: leg length and leg orientation (θ_L). Positive angles are in the counterclockwise direction.

The UCM hypothesis is more thoroughly described in previous work (Scholz and Schöner 1999; Tseng et al. 2002) but I will briefly explain how it pertains to my study. The UCM is a linearization of each of my mathematical functions that is estimated as the null space ($\vec{\varepsilon}$) of the Jacobian (J) of each function relative to a reference leg posture ($\vec{\Theta}^O$, Eq. 2.1).

$$0 = J(\vec{\Theta}^O) \cdot \vec{\varepsilon} \qquad (2.1)$$

The UCM analysis is a static analysis that is performed over successive hop cycles at a specific instant in time of the cycle and with respect to a reference leg posture. I performed the UCM analysis over successive hops at 1% increments of the hopping cycle. In each of my 100 UCM analyses, I defined my reference leg posture ($\vec{\Theta}^O$) as the average set of segment angles at that specific time bin in the hopping cycle. I then

projected the deviations of the segment angles ($\vec{\Theta}$) from this reference posture onto the null space ($\vec{\varepsilon}_i$) to resolve the fraction of deviations that did not affect the task, i.e. goal equivalent deviations ($\vec{X}_{GED}$, GED, Eq. 2.2). The remaining fraction was then deemed to be orthogonal to the null space and, hence, non-goal equivalent deviations ($\vec{X}_{NGED}$, NGED, Eq. 2.3).

$$\vec{X}_{GED} = \sum_{i=1}^{n} \vec{\varepsilon}_i^{\,T} \cdot (\vec{\Theta} - \vec{\Theta}^{O}) \cdot \vec{\varepsilon}_i \tag{2.2}$$

$$\vec{X}_{NGED} = (\vec{\Theta} - \vec{\Theta}^{O}) - \vec{X}_{GED} \tag{2.3}$$

The amount of variance per degree of freedom (*n*) parallel to the UCM was defined as goal equivalent variance (σ^2_{GEV}; Eq. 2.4).

$$\sigma^2_{GEV} = \frac{\sum \vec{X}^2_{GED}}{n \cdot N_{cycles}} \tag{2.4}$$

The amount of the variance per degree of freedom (*d*) orthogonal to the UCM was defined as non-goal equivalent variance (σ^2_{NGEV}; Eq. 2.5).

$$\sigma^2_{NGEV} = \frac{\sum \vec{X}^2_{NGED}}{d \cdot N_{cycles}} \tag{2.5}$$

To normalize for inter-subject variability, I calculated the Index of Motor Abundance (*IMA*), a metric for the amount of motor abundance that is selectively utilized to stabilize the performance variable (Tseng et al. 2002; Tseng and Scholz 2005). An IMA greater than zero indicates that the segment angles varied in a coordinated manner from hop to hop to minimize any destabilizing effect on the performance variable. An IMA equal to zero indicates that there was no coordinated interjoint compensation strategy for stabilizing leg length and orientation. An IMA less than zero indicates that

the majority of the small changes occurring at the level of the limb segments were coordinated to destabilize the performance variable. I calculated the IMA as (Eq. 2.6):

$$IMA = \frac{(\sigma^2_{GEV} - \sigma^2_{NGEV})}{(\sigma^2_{GEV} + \sigma^2_{NGEV})} \quad (2.6)$$

I calculated σ^2_{GEV}, σ^2_{NGEV} and IMA at 1% intervals during the contact and aerial phases of the hopping cycle for leg length and orientation control functions at 2.2, 2.8, and 3.2 Hz. Data were first divided into stance and aerial phase for each subject and then further divided into ten equal bins of 10% of each respective phase. Note that the sizes of the bins in the aerial phase are smaller than those in the stance phase.

2.2.5 Statistical Analysis

I hypothesized that: 1) subjects would stabilize leg length and leg orientation over the entire hopping cycle by coordinating local joint kinematics through selective use of motor abundance and 2) on average the selective use of motor abundance will increase with the increasing hopping frequency. To determine whether a performance variable was stabilized by local variables, I performed a Student's one-sample, one-tailed t-test ($\alpha = 0.05$) to test whether IMA was significantly greater than 0. This is denoted by the horizontal black line above the bins in Figure 2.5. To test whether increasing hopping frequency and difficulty resulted in increased IMA, I used a one-way repeated measures analysis of variance (ANOVA) to test for interaction effects of average IMA across time and frequency ($\alpha = 0.05$) and a post-hoc test with Bonferroni correction to determine which frequencies had different IMAs (as illustrated in figures 4 and 6). All statistical analyses were done using SPSS software (SPSS Inc.; Chicago, IL).

2.3 Results

2.3.1 Kinematics

The trajectories of the performance variables, leg length and orientation, were qualitatively conserved from hop to hop with only minor deviations from the mean throughout the entire hopping cycle (Figure 2.2a and 2.2b). Segment angle trajectories were also qualitatively conserved throughout the entire hopping cycle (Figure 2.2c, Table 2.1). Upon simple inspection, there did not appear to be an obvious strategy for coordination of segment angles to stabilize leg length or orientation. Shank and thigh segment angles at mid-stance became more vertically oriented as frequency increased ($p<0.01$) with no significant change in foot and pelvis segment angles (Table 2.1). This indicates that my subjects adopted a more upright posture as hopping frequency increased (Table 2.1).

2.3.2 GEV and NGEV results

GEV and NGEV components were calculated for each subject, hypothesis, and frequency condition (see Figure 2.3 for data from a representative subject). I observed a statistical trend among my subjects where the average total variance of the segment angles normalized per degree of freedom (GEV + NGEV) within a subject significantly increased with increasing hopping frequency for leg length ($p = 0.015$) and orientation stabilization ($p = 0.038$; Figure 2.4). GEV and NGEV were not averaged across subjects and shown here to illustrate the quality and trends of data from GEV and NGEV. While the relationship between GEV and NGEV was consistent across subjects, there was substantial intersubject variability in the magnitude of total variance. To normalize for

the intersubject variability while preserving the trend of the structure of variance, I used IMA as my metric.

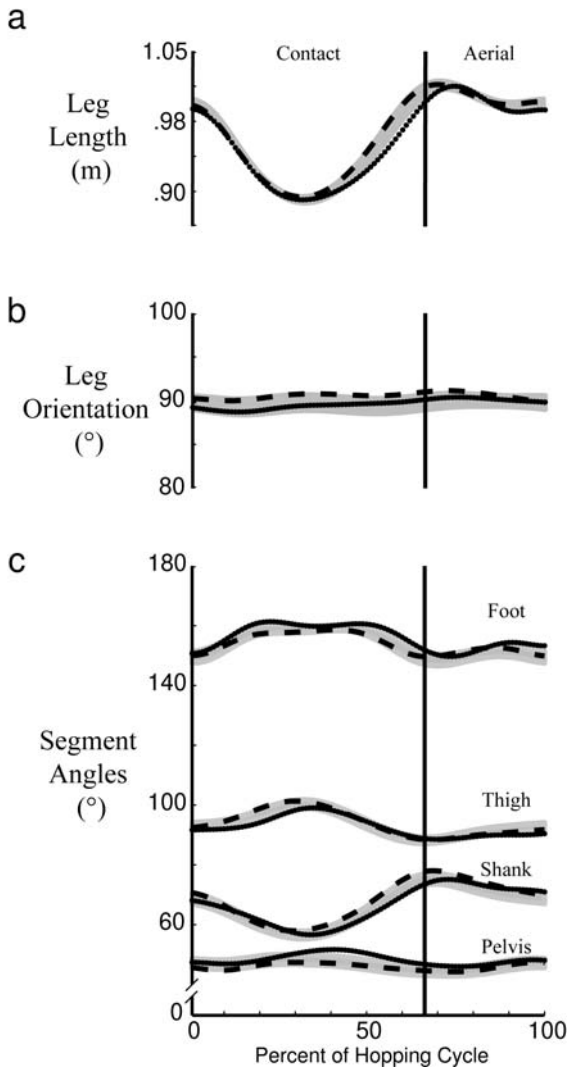

Figure 2.2. Kinematics data from a representative subject hopping at 2.2 Hz. Qualitatively, global variables **(a)** leg length and **(b)** leg orientation are highly conserved throughout the entire hopping cycle across all hops. **(c)** Local variables, segment angles, also showed little apparent variation from their mean trajectories. Grey shaded regions denote ±1 standard deviation from the mean trajectory (189 hops). Dashed and dotted lines are trajectories from two randomly selected hops.

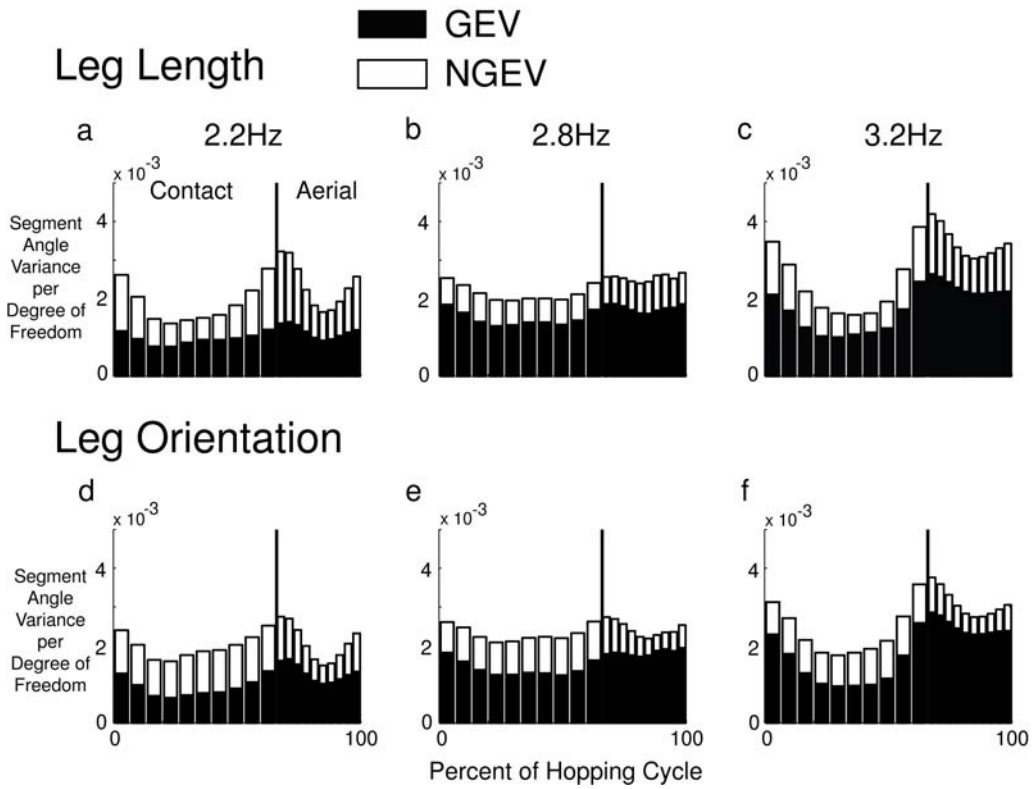

Figure 2.3. Goal equivalent variance (GEV, black) and non-goal equivalent variance (NGEV, white) from a representative subject

(a-c) relative to leg length stabilization and **(d-f)** relative to leg orientation stabilization across three frequencies.

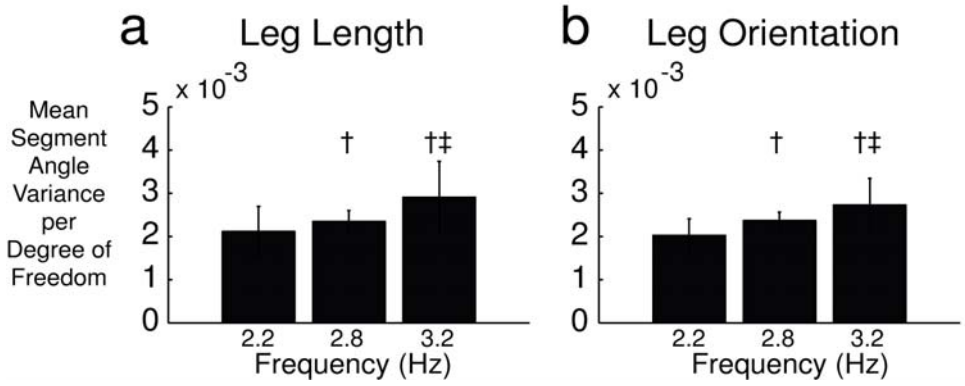

Figure 2.4. Average total segment angle variance (GEV+NGEV) from a representative subject

Average total segment angle variance **(a)** for leg length stabilization and **(b)** leg orientation stabilization across three frequencies. Average total segment angle variance for leg length and orientation stabilization increased with hopping frequency. †denotes significant difference from 2.2 Hz ($p<0.01$). ‡ denotes significant difference from 2.8 Hz ($p<0.01$). ($n = 167$).

2.3.3 IMA results

At the lowest hopping frequency of 2.2 Hz, the IMA for leg length stabilization was significantly greater than 0 ($p<0.01$) throughout nearly the entire hopping cycle indicating that interjoint coordination acted to stabilize leg length, denoted by the horizontal black bar over the bins (Figure 2.5a). IMA reached a peak around mid-stance (30-60% of stance). At 2.8 and 3.2 Hz, the IMA was statistically greater than 0 throughout the entire hopping cycle ($p<0.01$; Figure 2.5b & 2.5c). Average IMA for leg length control significantly increased with increasing frequency ($F_{(2,657)} = 48.763$, $p<0.001$; Fig 6a). Despite the overall increase in average leg length IMA with frequency, the individual IMA bins at mid-stance (30-60%) were not statistically different across the three hopping frequencies ($p>0.05$). The increase in average IMA was due to increases in bins at early and late stance phase and across aerial phase ($p<0.01$).

IMA for leg orientation at 2.2 Hz was greater than 0 during all of aerial phase and early stance phase ($p<0.01$, Figure 2.5d). There was also a noticeable rise in IMA during the latter portion of aerial phase (50-90% of aerial phase). At 2.8 and 3.2 Hz, I did not, however, observe any statistical difference in the average IMA for leg orientation across frequencies ($p=0.239$; Figure 2.6b) indicating the interjoint coordination strategy used to stabilize leg orientation did not change.

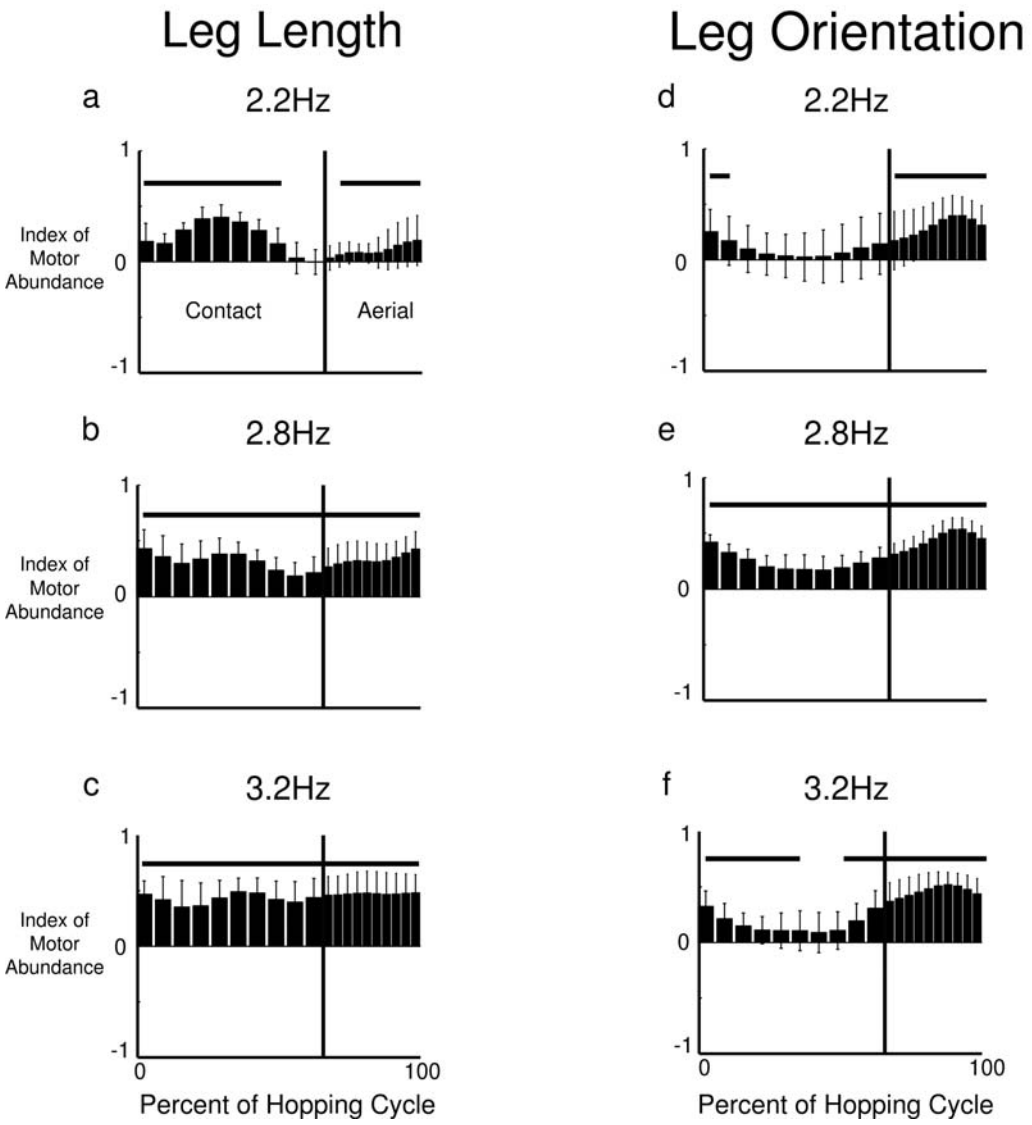

Figure 2.5. Index of Motor Abundance (IMA)

(a-c) leg length stabilization and **(d-f)** leg orientation stabilization across three frequencies. IMA for leg length stabilization in bins between 30-60% of stance phase remained unchanged across frequency. IMA for leg orientation stabilization in bins 50-90% of aerial phase remained unchanged across frequency. Solid horizontal bar indicates that the bin beneath it is > 0 ($p<0.05$). Data are IMA ±1 standard deviation averaged across all subjects.

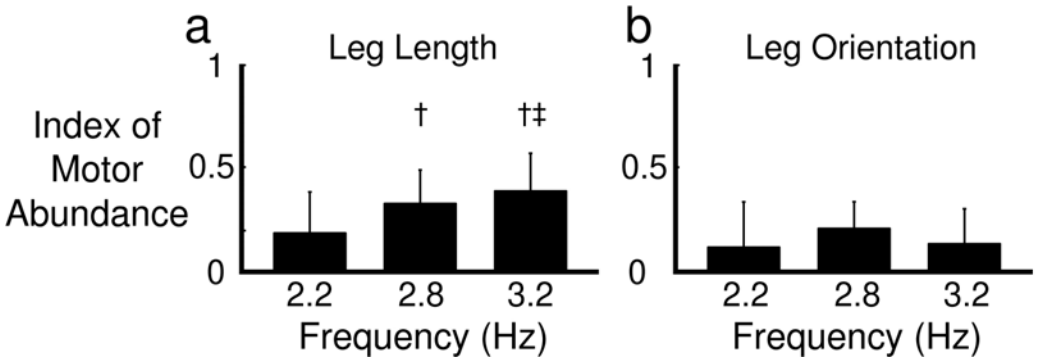

Figure 2.6. Average Index of Motor Abundance (IMA)

Average IMA **(a)** for leg length and **(b)** leg orientation at the three hopping frequencies. Average IMA for leg length increased with frequency Average IMA for leg orientation did not change with frequency. Data are average IMA ±1 standard deviation for all subjects and time bins. †denotes significant difference from 2.2 Hz ($p<0.01$). ‡ denotes significant difference from 2.8 Hz ($p<0.01$).

2.4 Discussion

Upon qualitative inspection, I did not observe any obvious patterns of inter-cycle variability in the trajectories of the segment angles, leg length, or orientation across all three hopping frequencies. Through my UCM analysis, however, my data indicate that my subjects selectively shaped the structure of segment angle variance to stabilize leg length and orientation from hop to hop. Quantifying the variance of the segment angles parallel (GEV) and orthogonal (NGEV) to the UCMs for leg length and orientation stabilization revealed a clear structure to the inter-cycle variance. At 2.2 Hz, there were strong phasic trends toward stabilizing leg length during mid stance and leg orientation during late aerial phase (Figure 2.5a and 5d). In contrast, when hopping at non-preferred frequencies 2.8 and 3.2 Hz, the majority of the segment angle variance was put into goal-equivalent angle space for stabilizing leg length (Fig 5b-c) with no significant frequency affect observed for stabilizing leg orientation (Fig 5e-f).

2.4.1 Are leg length and orientation stabilized?

Contrary to my predictions, leg length and orientation were not stabilized throughout the entire hopping cycle. The UCM analysis revealed temporal control of these performance variables at different key points in the hopping cycle. I found that leg length had peak stabilization during mid-stance of contact phase while leg orientation saw maximum stabilization during the aerial phase.

The spring-mass model has been extensively explored in biomechanics research involving hopping. Effective leg stiffness has been identified as a key determinant of spring-mass dynamics and varies directly with hopping frequency (Farley et al. 1993; Farley and Morgenroth 1999; Ferris et al. 2006). Specifically, I define leg stiffness (k_{leg}) as the ratio of change in vertical ground reaction force (ΔF) to the change in overall leg length (ΔL, Eq. 2.7):

$$k_{leg} = \frac{\Delta F_{Vert}}{\Delta L} \tag{2.7}$$

Consequently, control of leg length trajectories will directly affect the spring mass dynamics of hopping.

When hopping at 2.2 Hz, subjects had a tendency to maximize stabilization of leg length during mid-stance. I was unable to definitively test the reason for this phenomenon; however, it is likely related to the importance of mid-stance kinematics for determining spring-mass dynamics. Mid-stance is a critical time of the hopping cycle when joint flexion and leg forces generated against the ground reach a maximum (Farley et al. 1991). Mid-stance is also when joints transition from flexion to extension and reverses the direction of vertical CoM movement. A potential explanation for my results is that greater leg length control is required during periods of high potential for deviations

in leg length. Due to its trigonometric relationship with the segment angles, leg length is most sensitive to small changes in segment angles when the segments are more horizontally oriented, as in mid-stance when the joints are most flexed (Blickhan et al. 2007; Chang et al. 2009; Chang et al. 2008). Therefore, mid-stance represents a critical period during hopping when increased sensitivity of leg length to small variations in segment angles must be attenuated and stabilized through interjoint coordination. There is evidence that the control of limb kinematics selectively focuses stabilization near specific kinematic targets (Todorov and Jordan 2002). During 2.2 Hz hopping, mid-stance is the time when leg length is most vulnerable to local joint variations and therefore a likely kinematic target that requires stabilization.

The peak stabilization of leg length at mid-stance during 2.2 Hz hopping may also indicate the importance of minimizing muscle force variability on joint kinetics at this portion of the hop cycle. A shorter leg length equates to more flexed joints and a more crouched posture. As the posture becomes more crouched, the effective mechanical advantage of the muscles crossing the joints decreases and requires greater muscle forces to generate the same force on the ground (Biewener 1989; Biewener et al. 2004). Stabilizing leg length kinematics during mid-stance through interjoint coordination may be a mechanism for minimizing joint moments and therefore, muscle forces when they are at their peaks (Yen and Chang 2007; Yen et al. 2009; Yen and Chang 2010).

Recent neurophysiological studies support the idea of a neural representation for kinematic elements of the spring-mass model. Great insight was given by direct *in vivo* recordings of dorsal spinocerebellar tract (DSCT) neurons in the cat spinal cord as the leg was passively moved in space to mimic locomotion (Bosco and Poppele 2000; Bosco et

al. 2000; Poppele et al. 2002). DSCT neurons are known to bring converging sensory information to the areas of the cerebellum important for the control of locomotion. These findings showed that both leg length and orientation were represented in specific populations of neurons within the central nervous system at the level of the spinal cord. The evidence I present in this study suggests the possibility that a neuromechanical representation of leg length and orientation exists during human hopping. Furthermore, the nervous system may use a strategy to structure the variance of local segment angles to stabilize these performance variables as a way of reducing the degrees of freedom in control parameters.

Contrary to my first hypothesis, leg orientation was only stabilized in the aerial phase and early stance phase during 2.2 Hz hopping ($p<0.01$). Leg orientation at ground contact determines the position of the foot relative to the body (Blickhan 1989; McMahon 1990; McMahon and Cheng 1990). Intuitively, the control of leg orientation during aerial phase is important for determining how the body lands and its CoM trajectory after landing. This is exemplified by the control of a hopping robot where foot placement at ground contact determined the forward velocity of the robot (Raibert et al. 1984). In this under-actuated robot, leg orientation was calculated only during the aerial phase to ensure proper foot placement at contact. Passive dynamics were then relied upon to achieve the desired forward velocity during the contact phase. This suggests that leg orientation control in biological systems may be most important during the aerial phase, as I observed.

My findings also provided further temporal resolution within each hop cycle about when leg orientation is controlled within each locomotor phase. IMA increased

through the first half of aerial phase in 2.2 Hz hopping, reaching a peak approximately halfway through aerial phase and remained high throughout the latter half of aerial phase (Fig 5d). This is the portion of aerial phase that directly precedes foot placement at ground contact and determines the landing angle of the leg. Foot position at ground contact determines the forward acceleration of the body during stance, and by extension, the body's forward velocity and position (Raibert et al. 1984).

An interesting task alternation strategy between the stabilization of leg length and orientation can be seen when hopping at 2.2 Hz. This is most noticeable at mid-stance and aerial phase where the maximum stabilization of one performance variable is matched by the minimization of the other performance variable. A similar phenomenon was observed in a two finger force production task (Latash et al. 2001; Latash et al. 2002b; Scholz et al. 2002). A task alternation strategy was observed between force and moment stabilization over time due to orthogonal alignment of the UCMs. Similarly, my present results can be explained by the fact that the UCMs for leg length and orientation stabilization were nearly orthogonal to each other (mean over hopping cycle was 80.4°). Consequently, the locomotor control system might be choosing a strategy that alternately stabilizes one task at a time to maximize flexibility rather than to constrain itself to a smaller overlapping solution space where both tasks can be simultaneously achieved.

2.4.2 Effect of increased task difficulty on leg length and orientation stabilization

While I initially hypothesized that hopping in a mechanically unstable state at higher frequencies would require increased stabilization of both leg length and orientation, I only observed this effect on stabilization of leg length. Average IMA for leg length stabilization significantly increased with frequency, indicating that leg length was

increasingly stabilized through small compensatory adjustments of the segment angles ($p<0.001$; Fig 6a). One explanation for this observation is that locomotor systems operating at non-preferred frequencies require increased stabilization of global variables. Subjects walking at non-preferred step frequencies have increased metabolic cost and increased interjoint coordination variability while maintaining lower variability in global performance variables, e.g. head position (Holt et al. 1995; Jeng et al. 1997). Similarly, at increased hopping frequencies, I observed no change in leg length variability despite increased variability in shank and thigh segment angles (Table 2.1). These results translated into increased stabilization of leg length due to the structure of interjoint variability when hopping at non-preferred frequencies. Leg length may be inherently more stable at the preferred hopping frequency. Consequently, higher hopping frequencies may require more active stabilization of leg length.

Average stabilization of leg orientation did not appear to change significantly with frequency as I had initially predicted (Fig 6b). Stabilization remained highest during the latter half of aerial phase and was minimal during the stance phase at all frequencies. The unchanged timing and magnitude of peak stabilization of leg orientation at higher frequencies suggests no change in control strategy was required despite the energetically more difficult task of hopping in place at higher frequencies. In the control of a forward hopping monopod robot, control of toe position during the aerial phase is essential for controlling forward velocity of the locomotor system during stance phase (Raibert et al. 1984). Given that my subjects were asked to hop in place and therefore maintain a zero forward velocity across all conditions, a similar control strategy for leg orientation over different frequencies is not surprising.

That leg length stabilization was dependent on hopping frequency while leg orientation stabilization was independent can be further explained by considering the relationship between the vertical frequency of oscillation (ω) with leg stiffness (k_{leg}) and total body mass (m; Eq. 2.8 ; (see (Blickhan 1989; Farley et al. 1993; McMahon and Cheng 1990)):

$$\omega^2 = \frac{k_{leg}}{m} \tag{2.8}$$

Vertical leg stiffness (k_{vert}; Eq. 2.9) is similar to k_{leg} (Eq. 2.7) except that it relates changes in force and displacement in only the vertical direction despite the orientation of the leg, i.e. vertical force (ΔF_{vert}) with vertical displacement in center of mass (Δy_{vert}):

$$k_{vert} = \frac{\Delta F_{vert}}{\Delta y_{vert}} \tag{2.9}$$

Δy_{vert} is a function of change in leg length (ΔL), initial leg length at contact (L_o), and leg orientation at initial contact (θ_L). So equation 2.9 can be rewritten as (Eq. 2.10):

$$k_{vert} = \frac{\Delta F_{vert}}{\Delta L + L_o(1 - \sin\Theta_L)} \tag{2.10}$$

Hopping in place results in a θ_L of approximately 90^o resulting in Δy_{vert} being roughly equivalent to ΔL (Eq. 2.11):

$$\Delta y_{vert} \cong \Delta L \tag{2.11}$$

Therefore, in the special case of hopping in place, k_{vert} and k_{leg} (Eq. 2.7) become mathematically equivalent. (Eq. 2.12):

$$\omega^2 m = k_{leg} = k_{Vert} = \frac{\Delta F_{Vert}}{\Delta L} \tag{2.12}$$

While control of ΔL can contribute to determining the oscillation frequency in this special case, control of leg orientation cannot. This agrees with the presence of a frequency effect I observed for leg length stabilization and the lack of a frequency effect for leg orientation control. My observations at 2.2 Hz likely represented a minimum control strategy required for hopping. Increasing the hopping frequency required increased leg length control to maintain non-preferred leg stiffness. At zero forward velocity, i.e. when $\Theta_L \cong 90^\circ$, the control of leg orientation does not influence $k_{vert;}$ therefore, any changes in oscillation frequency were not influenced by leg orientation control. However, I predict that control of leg orientation is likely to have frequency effects in cases where $\Theta_L < 90^\circ$, as is the case in forward running and hopping when velocity is greater than zero (Farley et al. 1993).

2.4.3 Potential mechanisms for stabilization of performance variables

Stabilization of kinematic performance variables requires a coordinated interjoint response to a perturbation. For example, consider that the system may have a desired value for leg length. If the person experiences excessive ankle flexion, overall leg length would decrease. Interjoint compensation for this ankle deviation can occur through either knee extension, hip extension, or some combination of the two. A biarticular muscle that flexes the ankle and extends the knee could achieve this. Yet, there are no such biarticular muscles in the human leg that can accomplish this despite the obvious fact that simultaneous ankle flexion and knee extension is possible. This suggests that neural reflex pathways may be responsible for such compensatory movements. A similar stabilization problem has been observed in the shoulder-elbow complex of the pectoral limb (Cabel et al. 2001; Kurtzer et al. 2006; Sangani et al. 2007). The biceps brachii

muscle is a biarticular muscle responsible for elbow flexion and shoulder adduction which acting alone, would destabilize arm length. Yet, elbow flexion and shoulder adduction are actively decoupled to compensate for perturbations to arm length. Heteronymous reflex pathways were proposed for stabilizing arm length (Cabel et al. 2001; Kurtzer et al. 2006; Sangani et al. 2007). In the lower extremities, numerous excitatory and inhibitory pathways connect different muscle groups in a complex network, many of which have yet to be identified. Heteronymous reflexes have been found between muscles in the quadriceps group and muscles in the triceps surae in the hind limbs of cats (Wilmink and Nichols 2003). They showed significant excitatory length feedback that linked the vastus muscles to the soleus muscle. Furthermore, a recent neuromechanical model of the cat hindlimb indicated that heteronymous joint reflexes improved stabilization of limb posture over single joint reflexes (Bunderson et al. 2007). While further studies on the contribution of heteronymous reflexes to limb stabilization for locomotion are needed to confirm the ubiquity of these results for other mammalian systems, I hypothesize that humans may use similar reflexes for leg length compensation. For example, a flexion perturbation applied at the knee could stretch the quadriceps muscle group and trigger a heteronymous excitation of the triceps surae muscle group, resulting in a compensatory ankle extension.

Alternatively, task stabilization could be achieved through the passive mechanical actions of isometrically activated biarticular muscles or through interaction torques. There is evidence that interaction torques and multi-articular muscles in the upper limbs may play an important role in compensation to achieve task stabilization (Martin et al. 2005; Martin et al. 2003; 2004). Interaction torques have also been suggested to have a

major role during swing phase in humans (Hoy and Zernicke 1985). Biarticular muscles and interaction torques may also play a role in lower limb task stabilization during locomotion. While the current data set and study cannot draw definitive conclusions as to the mechanisms, future work should try to partition the role of neural and mechanical compensation strategies.

2.4.4 Conclusions

Extensive research modeling bouncing gaits as spring-mass systems, specifically hopping in place, provided an ideal context to study the stabilization of known biomechanical performance variables through intralimb compensation. I found that at 2.2 Hz, leg length was stabilized during mid-stance when small joint angle deviations can most easily destabilize leg length. The control of leg orientation was highest during the latter half of aerial phase to stabilize landing leg orientation and toe position at foot contact, which determines the body's forward velocity over the stance phase. Overall stabilization of leg length increased as the difficulty of hopping increased with higher frequencies. I did not observe any change in leg orientation control with increasing frequency most likely because forward velocity remained unchanged across conditions. While previous research has suggested the importance of leg length and orientation as global performance variables during hopping, I show for the first time that the joints simultaneously coordinate and reject cycle-to-cycle perturbations for the purpose of stabilizing leg kinematics during locomotion. This further supports the likelihood that a neuromechanical representation of a low degree of freedom spring–mass model can be used by the nervous system to control the legs during hopping. Understanding how able-bodied persons exploit neuromechanical redundancy in the legs to stabilize whole body

locomotor performance can provide important insights into developing goal-oriented strategies for gait rehabilitation of persons with pathologically compromised leg control.

CHAPTER 3

EFFECT OF ACCURATE FOOT PLACEMENT TASK CONSTRAINTS ON LEG LENGTH AND LEG ORIENTATION STABILIZATION STRATEGIES

3.1 Introduction

Locomotion may seem like a common, everyday task but the difficulty of this task is always changing as we are constantly being perturbed. Yet, the human locomotor system is adaptable and robust, allowing for quick and effective compensation to these perturbations to achieve stable locomotion. One reason the human locomotor system is adaptable is due to the kinematic redundancy of the locomotor system which allows access to a number of different joint configuration solutions for a task goal. But how exactly is this adaptability exploited to maintain stable locomotion when the task difficulty increases?

Human hopping in place is an excellent locomotion model to study because the center of mass dynamics of bouncing gaits can be approximated by a low degree of freedom spring-mass model (Blickhan 1989; Farley et al. 1993; McMahon 1984; McMahon and Cheng 1990). The low number of components that make up this model makes it useful for identifying potential limb level performance variables. Two kinematic variables in particular, leg orientation and leg length, are of particular interest as there are biomechanical, computational, and neurophysiological evidence for their control (Blickhan 1989; Bosco and Poppele 2000; Bosco et al. 2000; Ivanenko et al. 2007; Ivanenko et al. 2008; Lacquaniti et al. 1990b; McMahon and Cheng 1990). More recently, both leg orientation and leg length have been shown to be stabilized individually

through the coordination of segment angles during human hopping (Auyang et al. 2009). As such, stabilization of leg length or leg orientation during human hopping is a good model for studying the effects of varying task difficulty.

The locomotor system is capable of adapting to changing conditions and task difficulties while maintaining invariant task performance variables. When confronted with environmental perturbations, such as differences in surface stiffnesses, subjects are able to continue preserving a stable center of mass trajectory and effective leg stiffness (Ferris et al. 1999; Ferris et al. 1996; Moritz and Farley 2003). Mechanically constraining individual joint kinematics and kinetics also yields invariant center of mass trajectories and effective leg stiffnesses (Chang et al. 2008; Ferris et al. 2006). In cases where neuromuscular injuries are involved, animals maintain invariant leg orientation or leg length trajectories despite significantly higher individual joint variability after injury (Chang et al. 2009). Despite the obvious conservation of performance variables even when locomotion is made more difficult by task constraints, how the locomotor system achieves this conservation of performance variables when faced with different task difficulties during locomotion is not clear.

One method for investigating performance variable stabilization is through the use of an Uncontrolled Manifold (UCM) analysis. The UCM is a space of solutions made up of local variable combinations that achieve a given value of a performance variable. Performance and local variables are task specific. Performance variables can be defined as a function of the local variables. The UCM analysis is an analysis of local variable variance structure to test if more variance is aligned along the UCM space of solutions or away from it (Auyang et al. 2009; Scholz and Schöner 1999; Tseng and Scholz 2005). As

the structure of local variable variance is more aligned with the UCM, the performance variable trajectory is made more invariant, or stabilized, from cycle to cycle. Using a UCM analysis, several studies have shown examples of the changes in the alignment of the local variable variance structure relative to the performance variable manifold as task difficulty increases. More upper extremity joint variance is structured to stabilize endpoint effector position as task difficulty increases (Tseng et al. 2003). Studies involving sit-to-stand tasks revealed that limiting the base of support results in increased stabilization of center of mass movement (Scholz et al. 2001; Scholz and Schöner 1999). I have also shown that hopping at non-preferred frequencies causes increased stabilization of leg length through more alignment of the segment angle variance structure (Auyang et al. 2009). I concluded that hopping at non-preferred frequencies altered the task difficulty for maintaining a stable leg length trajectory but had no effect on leg orientation. This study will test whether altering task difficulty to specifically affect leg orientation stabilization will result in a similar response in structuring of segment angle variance to stabilize leg orientation. I will alter the task difficulty by changing the landing target area sizes.

The purpose of this study is to investigate how humans adjust segment angle variance structure to stabilize leg length or leg orientation when they are presented with increasingly difficult locomotor tasks that only affect leg orientation. Specifically, I limited the landing area of my hopping subjects by projecting three targets sizes on the ground. I predicted that stabilizing leg orientation would be critical for hopping into smaller targets. Since cycle to cycle deviations in leg orientation can lead to landing outside the target area, I hypothesize that segment angle variance will need to be

structured such that the cycle to cycle deviations of leg orientation are less as target size decreases. As cycle to cycle deviations of leg length will not help in landing into smaller target areas, I hypothesize that changes in target size should have little to no effect on stabilization of leg length.

3.2 Methods

3.2.1 Subjects

Eleven healthy human subjects with no prior history of lower extremity injuries volunteered for this study (6 males, 5 females, mean(SD) age = 27(5) years, mass = 60.5(10.1)kg). All subjects gave informed consent prior to participating in this study as approved by the Georgia Institute of Technology's Human Subjects Institutional Review Board.

3.2.2 Experimental Protocol

I made anatomical measurements and placed eight retroreflective markers on anatomical landmarks on each of the lower extremities using a modified Helen Hayes marker set (anterior superior iliac spine, posterior superior iliac spine, thigh segment, lateral femoral epicondyle, shank segment, lateral malleolus, head of the second metatarsal phalangeal joint, and calcaneus). Subjects hopped in place on one-leg at 2.2Hz for three trials per target condition (large, medium, and small). Hopping frequency was determined based on previously reported preferred hopping frequencies (Farley et al. 1991). The order of the target conditions was randomized for each subject. Subjects matched the prescribed hopping frequency to the beat of an audible metronome, with a minimum of thirty second practice period to become familiar with hopping at the

prescribed frequency and target conditions. Each data collection trial lasted approximately thirty seconds. Each subject stood in the center of the target on the force platform and crossed their arms over their chest and hopped on their right leg. Approximately 190 hops were analyzed per subject per target condition.

3.2.3 Target Sizes

I used three target sizes to vary task difficulty. The size of each target was calculated based on desired Index of Difficulty (ID) and Fitts' law, a logarithmic relation between the ratio of twice the travel distance and the target width (Fitts 1954; Fitts and Peterson 1964). From a previous study, I determined the travel distance as the average maximum toe height from the ground for hopping in place at 2.2Hz (Auyang et al. 2009). I chose a linear increase in ID: .25 (easiest), .50, and 1.0 (most difficult). The resulting target sizes were .25m^2, 0.063m^2, and 0.01m^2, respectively.

3.2.4 Kinematics and Kinetics

I used a five camera motion-analysis system (120Hz; Vicon Motion Systems; Los Angeles, CA) to capture kinematic marker data. I filtered data using a zero phase shift fourth-order Butterworth low-pass filter with a 10Hz cut-off frequency. I calculated four sagittal plane segment angles (foot, shank, thigh, pelvis) with respect to horizontal with software coded in Matlab (Mathworks, Natick, MA) using the toe and anterior superior iliac spine (ASIS) marker positions and the calculated ankle, knee, and hip joint centers to create a linked segment kinematic model. I determined ground contact and liftoff events using a force platform (1080 Hz; AMTI; Watertown, MA) by detecting when the vertical ground reaction force crossed a threshold of 32 N.

3.2.5 Uncontrolled Manifold Analysis

An Uncontrolled Manifold analysis was used to quantify whether segment angle variance was purposefully structured to stabilize leg orientation or leg length from cycle to cycle variance. Specifics of this analysis can be found in Section 2.2.4.

3.2.6 Electromyography

I did a post-hoc collection of electromyography (EMG) data from five of my original subjects. The protocol was repeated as described earlier except with the collection of EMG from seven muscles of the right leg: tibialis anterior (TA), lateral gastrocnemius (LG), medial gastrocnemius (MG), vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), and the long head of the biceps femoris (BF). Data were collected using a wireless EMG system (1080Hz, Noraxon TeleMyo 2400T G2). EMG data were band pass filtered from 10-500Hz, rectified, and low pass filtered at 10Hz. EMG data for each channel were normalized to the peak activity recorded during the large hopping condition for that channel. Burst duration and amplitude were calculated for each muscle. A coherence analysis was performed between VL and LG, VL and MG, RF and LG, and RF and MG to test whether there was significant coactivation between the tested muscles (Halliday et al. 1995).

3.2.7 Statistical Analysis

A Student's one sample t-test ($\alpha = 0.05$) was used to test whether normalized total variance of segment angles changed with target difficulty. The same test ($\alpha = 0.05$) was used to test for significant differences in normalized leg orientation or leg length GEV and NGEV with target difficulty. To determine whether a performance variable was stabilized by local variables, I performed a Student's one-sample, one-tailed t-test ($\alpha =$

0.025) to test whether IMA was significantly greater than 0. This is denoted by the horizontal grey line above the bins. To test whether target size caused changes in IMA, I used a repeated measures analysis of variance (ANOVA) to test for interaction effects of average IMA across time and target size ($\alpha = 0.05$) and a post-hoc test with Bonferroni correction to determine which targets had different IMAs. A bivariate linear correlation was used to test whether there was a linear relationship between leg orientation and leg length IMA. I used a repeated measures analysis of variance (ANOVA) to test for the effect of target size on mean EMG activity and EMG burst duration. All statistical analyses were done using SPSS software (SPSS Inc.; Chicago, IL).

3.3 Results

3.3.1 Kinetics

Lower limb joint torque impulses showed no statistical difference between different target conditions (n = 11). Joint torque impulses were normalized for each subject based on subject weight and the anatomical leg length measured from the anterior superior iliac spine to the medial malleolus. Ankle extensor torques for large (0.176±0.026), medium (0.178±0.031), and small (0.177±0.027) targets showed no statistical difference ($p = 0.988$). Knee extensor torques for large (0.534±0.012), medium (0.049±0.02), and small (0.054±0.019) targets showed no statistical difference ($p = 0.786$). Hip extensor torques for large (0.033±0.011), medium (0.018±0.015), and small (0.027±0.021) targets showed no statistical difference ($p = 0.086$).

3.3.2 UCM Results

Total segment angle variance

Change in total segment angle variance relative to the large target condition was calculated for the medium and small target conditions (n = 11). Total segment angle variance significantly increased as the target size got smaller ($p \leq 0.05$, Figure 3.1). Change in GEV and NGEV components relative to the large target condition were calculated for leg length and orientation for the medium and small target conditions (n = 11, Figure 3.2). For leg orientation, as target size decreased, the NGEV component of variance did not change while the GEV component of variance significantly increased with task difficulty ($p \leq 0.05$, Figure 3.2b and 3.2d). For leg length, I observed the opposite, with no change in GEV and a significant increase in NGEV with task difficulty ($p \leq 0.05$, Figure 3.2a and 3.2c).

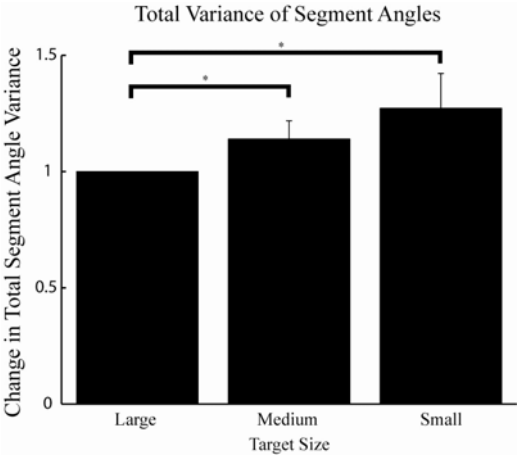

Figure 3.1 Total segment angle variance normalized to large target condition. Bars are the averaged total variances for all subjects with ±1 standard deviation. Total variance increased for both leg orientation and leg length as target size decreased. *denotes significant difference ($p<0.05$).

Leg length stabilization

IMA allows us to analyze variance structure across subjects. In the large target condition, leg length showed significant stabilization during most of stance (0-80% of stance) and late aerial phase (70-100% of aerial phase, $p<0.01$). Peak stabilization

occurred at midstance (p≤0.01, Figure 3.3a). As target size decreased, the period of leg length stabilization decreased to 30-70% of stance in the medium target condition (Figure 3.3b) and 40-60% stance for the small target (p≤0.01, Figure 3.3c). Peak stabilization remained at midstance. Average leg length IMA decreased with smaller targets and significantly decreased between the large and small target conditions (p = 0.03, Fig 3.4).

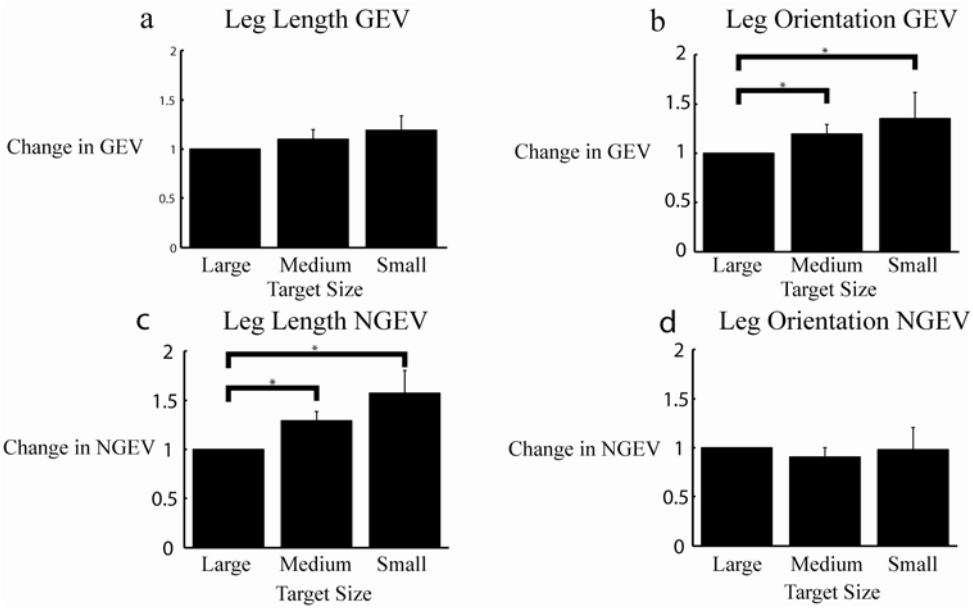

Figure 3.2 Goal equivalent variance (GEV) and non-goal equivalent variance (NGEV) Goal equivalent variance (GEV) and non-goal equivalent variance (NGEV) normalized to large target condition for the three target conditions for (**a** & **c**) leg length and (**b** & **d**) leg orientation. Bars are the averaged total variances for all subjects with ±1 standard deviation. Leg length NGEV and leg orientation GEV increased for medium and small target condition compared to large target condition. *denotes significant difference (p<0.05).

Leg orientation stabilization

In the large target condition, leg orientation was significantly stabilized during 0-20% and 90-100% of stance and all of aerial phase (p≤0.01, Figure 3.3d). Peak stabilization occurred at mid-aerial phase. As target size decreased to the medium target, the period of leg orientation stabilization increased to 0-30% and 70-100% of stance in addition to all of aerial phase (p≤0.01, Figure 3.3e). With the small target, I saw

significant stabilization of leg orientation throughout the entire hopping cycle ($p \leq 0.01$, Figure 3.3f). Average leg orientation IMA showed an increasing trend with smaller targets and showed a significant increase between the large and small target conditions ($p = 0.02$, Figure 3.4).

Leg length and leg orientation relationship and sensitivity

Leg length and leg orientation IMAs showed a significant negative linear correlation ($p = 0.03$, Figure 3.5). Leg orientation IMA did not increase linearly with index of difficulty. Rather it increased linearly with the target area. Also, regardless of target size, the anterior/posterior error in the foot placement during the contact phase showed no significant differences ($p = 0.08$). A sensitivity analysis showed that leg orientation was most sensitive to changes in shank and thigh angles. The average coefficients (sd) for the leg orientation Jacobian for the foot, shank, thigh, and pelvis segments are: 0.08(0.012), 0.36(0.05), 0.46(0.04), and 0.07(0.016).

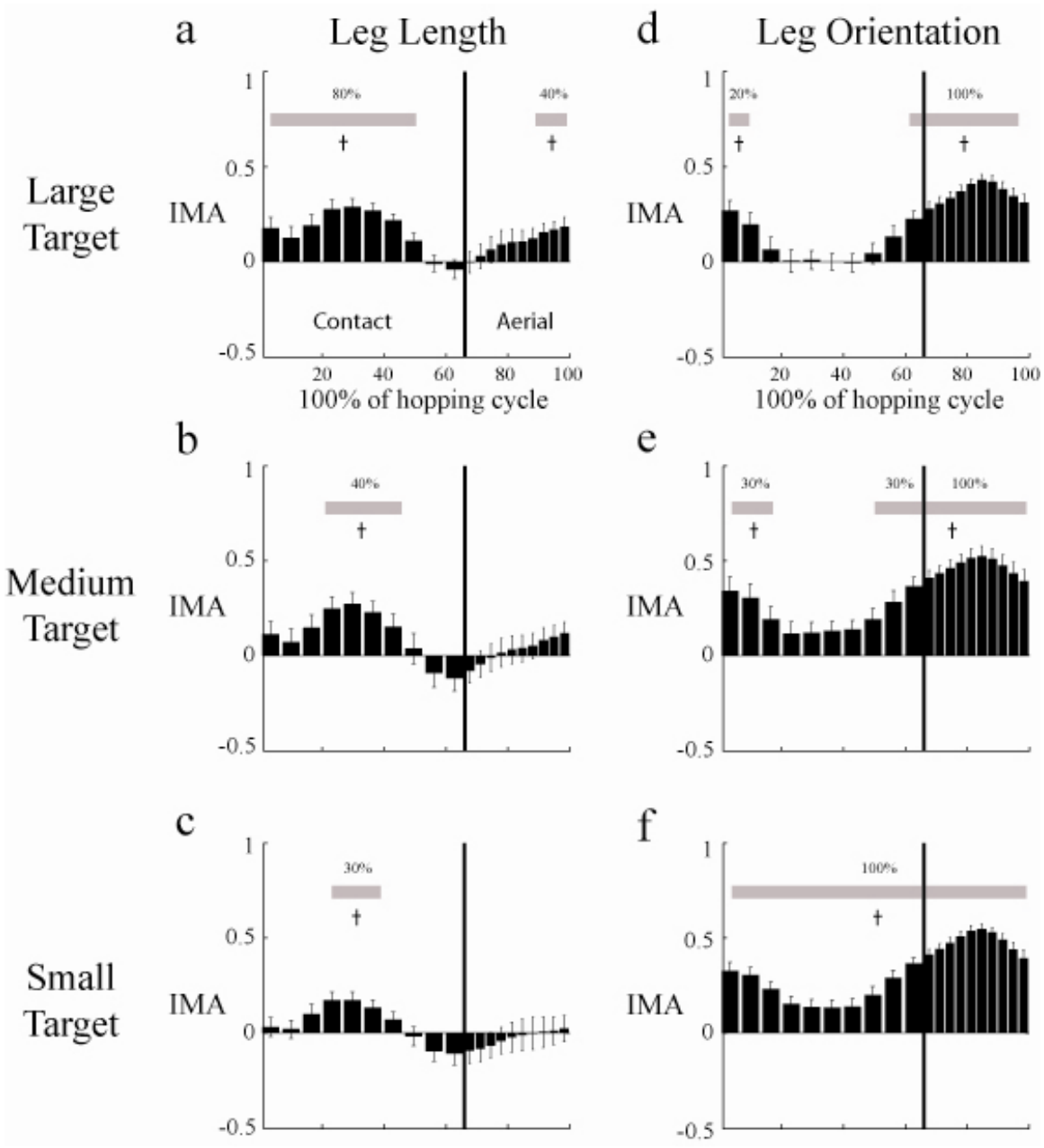

Figure 3.3 Index of Motor Abundance (IMA)

Index of Motor Abundance (IMA) **(a-c)** for leg length stabilization across three target conditions. **(d-f)** IMA for leg orientation stabilization across three target conditions. Bars are the averaged IMA for 10% intervals in contact and aerial phase. (n = 11) with ±1 standard deviation. Leg length stabilization period decreased with decreasing target size but remained stabilize at midstance. Leg orientation stabilization period increased with decreasing target size. Gray bar denotes period where IMA was significantly greater than 0 ($p<0.01$).

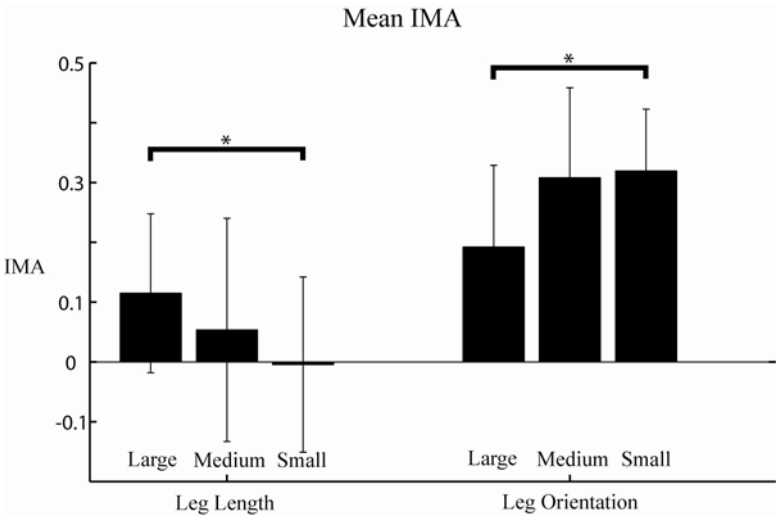

Figure 3.4 Average Index of Motor Abundance (IMA)
Average Index of Motor Abundance (IMA) for leg orientation and leg length for the three target conditions. Bars are the averaged IMA for all subjects and bins with ±1 standard deviation. Average stabilization of leg length decreased from large to small target while leg orientation stabilization increased from large to small target. *denotes significant difference ($p<0.05$).

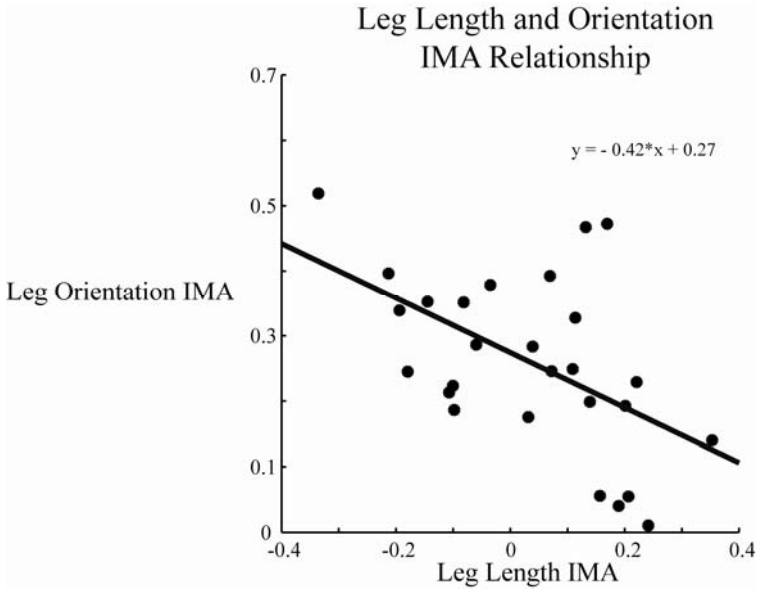

Figure 3.5 Leg orientation and leg length IMA relationship.
Leg orientation and leg length showed a significant negative linear correlation ($p = 0.03$). Increases in leg orientation IMA with decreases in leg length IMA corresponds with increases in task difficulty.

3.3.3 EMG

EMG data were collected from five of the eleven subjects in a separate post-hoc collection. Peak activation of all muscles recorded, except tibilas anterior, occurred at approximately mid-stance (Figure 3.6). During stance phase, there was a significant increase in mean muscle activity of the LG, MG, VM, VL, and RF muscles with increased difficulty ($p \leq 0.05$). TA activity decreased during stance phase as difficulty increased ($p \leq 0.05$, Figure 3.7). There was no statistical change in BF activity ($p > 0.05$). There were no significant changes in muscle activity during aerial phase in any of the muscles across target conditions (Figure 3.7b). The onset, offset and duration of muscle activity during both stance (Table 3.1 and Figure 3.7c) and aerial phase (Figure 3.7d) for all muscles recorded also showed no significant changes with target conditions.

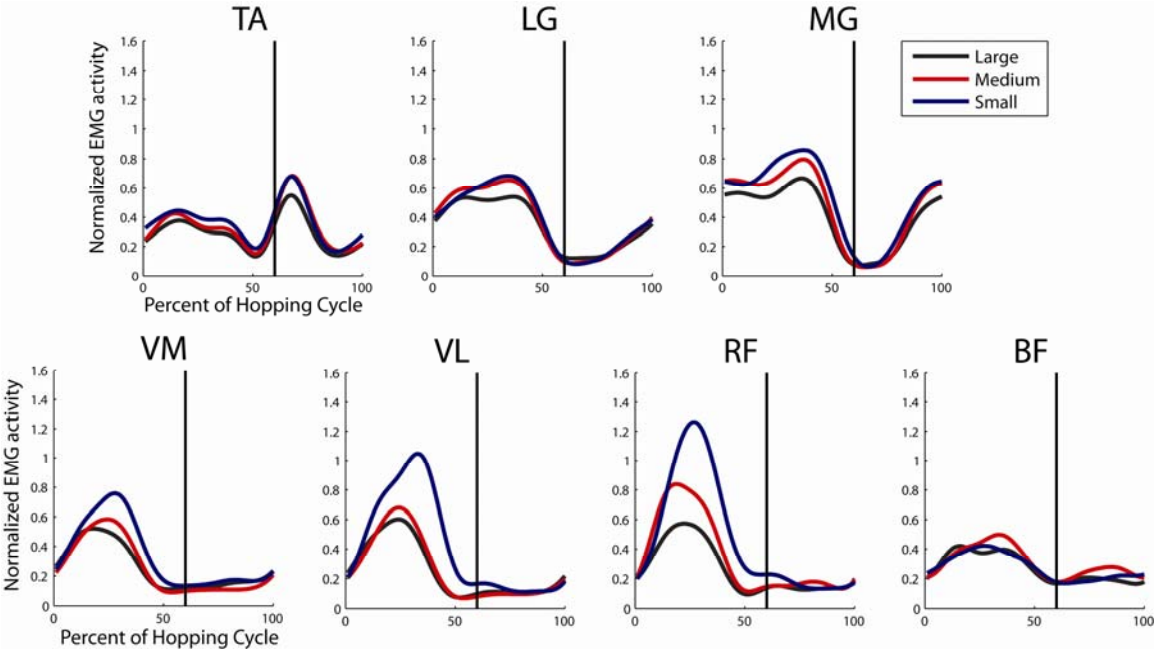

Figure 3.6 Average normalized EMG activity
Average normalized EMG activity for LG, MG, VL, VM and RF across the three target conditions for 100% of the hopping cycle. Muscle activity increased with target conditions.

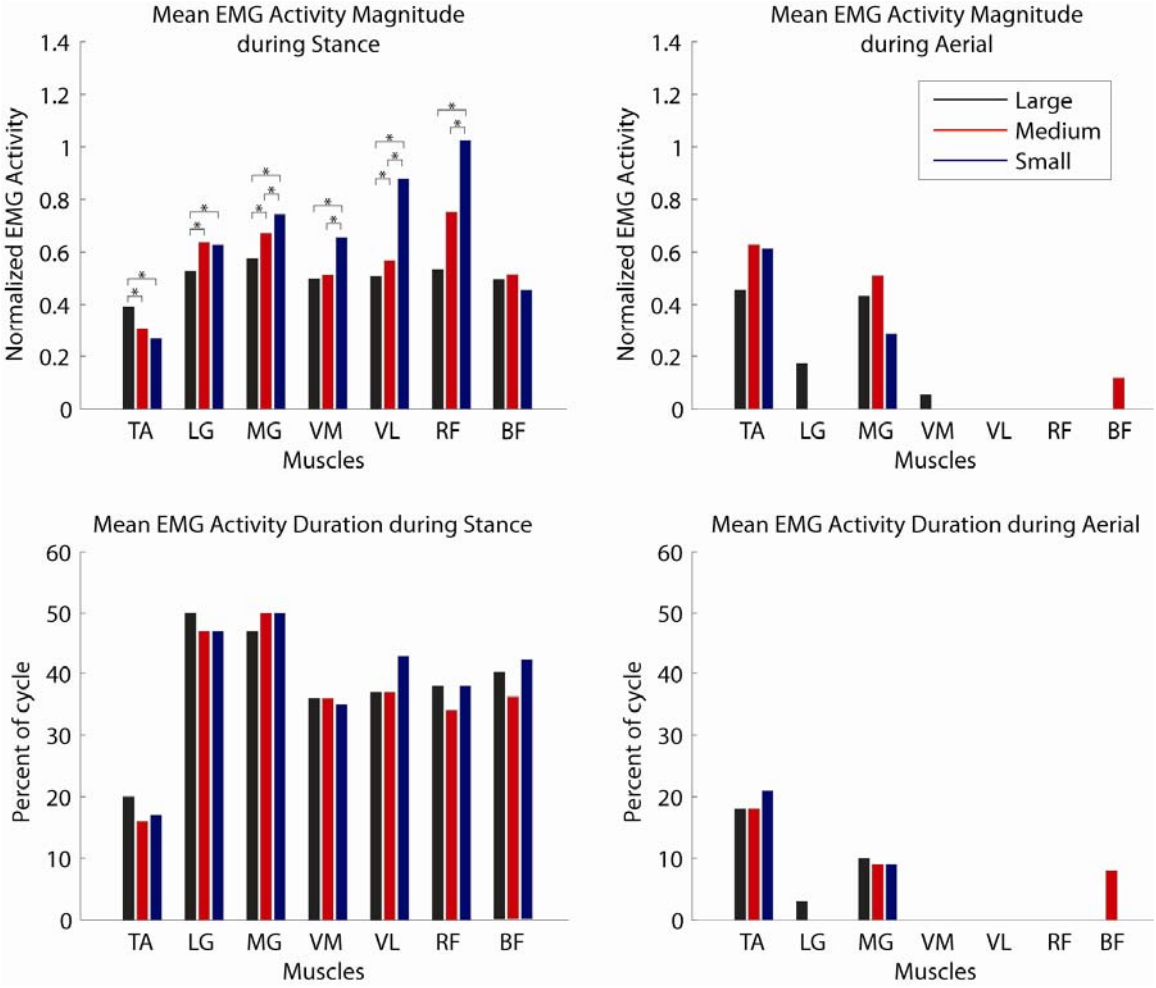

Figure 3.7 Average EMG burst activity magnitude and duration

(**a-b)** EMG burst activity magnitude and (**c-d**) EMG burst duration during stance and aerial phase for the three targeting conditions. Magnitude of activity increased for all muscles in more difficult target conditions compared to large condition except for TA which showed a significant decrease. No change was observed for burst duration. *denotes significant difference ($p<0.05$).

Table 3.1 Mean of EMG activity onset, offset, and duration during stance. Average percent of the cycle for EMG activity onset, offset, and duration (in percent, calculated as difference from offset and onset) for each target condition during stance phase.

		Onset (%)	Offset (%)	Duration (%)
TA				
	Large	7	27	20
	Medium	7	23	16
	Small	9	26	17
G				
	Large	1	51	50
	Medium	2	49	47
	Small	1	48	47
MG				
	Large	1	48	47
	Medium	1	51	50
	Small	1	51	50
VM				
	Large	1	37	36
	Medium	6	42	36
	Small	8	43	35
VL				
	Large	3	40	37
	Medium	5	42	37
	Small	4	47	43
RF				
	Large	2	40	38
	Medium	6	40	34
	Small	6	44	38
BF				
	Large	7	47	40
	Medium	11	47	36
	Small	9	51	42

3.4 Discussion

In this study I explored how the neuromechanical system stabilizes leg orientation and leg length during human hopping when the task is made more difficult. Using Fitts' Law, I was able to determine landing target areas of three sizes that would fit a linear increase in difficulty. A UCM analysis was used to determine whether leg length or orientation was stabilized through structuring segment angle variance during human hopping. The control condition IMA data of my current study, hopping at 2.2Hz in the

large target was similar with previous IMA findings for 2.2Hz hopping in place with no target (Auyang et al. 2009). Peak periods of stabilization for leg orientation and leg length occurred at similar points in the hopping cycle as with no target hopping (Figure 3.3a and 3.3d). By choosing a targeted hopping task and increasing task difficulty by decreasing target size, I selectively placed more importance on achieving a repeatable, invariant leg orientation trajectory and less importance on leg length.

3.4.1 Effects of task difficulty on performance variable stabilization

Low degree of freedom performance variables such as leg orientation and leg length are stabilized through a high dimensional kinematically redundant system made up of multiple segment angles. In turn, the variance in these angles has a significant effect on the leg orientation or leg length. In order to achieve an invariant or stable performance variable, one strategy is to minimize the variance of the local variables, i.e. minimize the total variance of all segment angles (Cusumano and Cesari 2006). My results show that subjects actually increased total segment angle variance when task difficulty increased (Figure 3.1). Another strategy by which a stable performance variable can be achieved is through structuring the variance of the local variables (Cusumano and Cesari 2006; Latash 2000; Scholz and Schöner 1999). The use of a UCM analysis allowed us to quantify how the segment angle variance was structured relative to leg length or orientation stabilization. I found significant changes with the variance structure as task difficulty increased. Supporting my hypothesis, segment angle variance was increasingly structured to stabilize leg orientation as task difficulty increased (Figure 3.4b). I also hypothesized no change in leg length IMA with task difficulty because it should not have been affected by the increase in task difficulty. I rejected this hypothesis since average

IMA for leg length actually decreased with increased task difficulty (Figure 3.4a). This decrease is likely due to the orthogonality of the leg orientation UCM relatively to the leg length UCM. This will be discussed later in section 3.4.4.

Changes in IMA can be attributed to the relative amounts of variance partitioned into Goal-Equivalent Variance (GEV) and Non-Goal-Equivalent Variance (NGEV). The increase in leg orientation IMA was due solely to an increase in the GEV component (Figure 3.2b) and no change in the NGEV (Figure 3.2d) component. This means that the increase in total segment angle variance with increased task difficulty (Figure 3.1) acted to stabilize leg orientation. In contrast, for leg length, the increase in total segment angle variance resulted entirely in an increase of the NGEV component (Figure 3.2c) while not affecting the GEV component (Figure 3.2c).

A more detailed look at leg orientation and leg length stabilization throughout the hopping cycle revealed that peak stabilization for leg orientation and leg length occurred at mid-stance and mid-aerial phase respectively during the large target hopping condition. The phase and amplitude of peak stabilization for both did not change as task difficulty increased (Figure 3.3). Leg length was stabilized throughout most of the hopping cycle while leg orientation was stabilized at the beginning and end of stance phase and all of aerial phase. These findings are similar to the leg orientation and leg length IMA profiles found in hopping in place at 2.2Hz with no target (Auyang et al. 2009). This shows that hopping in a large target area that provides a larger area than the average hopping distribution observed during non-targeted 2.2Hz hopping requires very similar control and more importantly, is not anymore difficult than the unconstrained task.

As task difficulty increased, leg length IMA decreased across the entire hopping cycle (Figure 3.3a-c). This resulted in a smaller window of time in which leg length was stabilized. Yet, despite the overall decrease in IMA, peak stabilization of leg length persisted at mid-stance even at the most difficult condition (small target). Mid-stance is an important period to stabilize leg length during hopping in place because it is then that leg length is most sensitive to small changes in segment angles (Auyang et al. 2009). It is also the point in the hopping cycle where there is maximum joint flexion and when peak forces are generated (Farley et al. 1991). A more flexed posture decreases the effective mechanical advantage of the muscles crossing joints and would require higher muscle forces to result in the same ground reaction force (Biewener 1989; Biewener et al. 2004). The stabilization of leg length at midstance likely limits peak deviations in joint moments when forces are at their peak. The results of this study provide further support for the importance of leg length stabilization at midstance. Despite the overall decrease of leg length stabilization throughout the whole cycle as difficulty increased, leg length remained stabilized at mid-stance.

For leg orientation, as task difficulty increased, IMA increased across the entire cycle except around the peak in aerial phase where it remained high (Figure 3.3d-f). Control of leg orientation during late aerial phase is important for foot placement at ground contact and for determining forward velocity of the spring-mass pendular dynamics (Raibert et al. 1984). As the task difficulty increased and more accurate foot placement became more critical to performance, adjustments only in the aerial phase may no longer be enough to accurately land in the smaller targets and deviations of leg orientation in other parts of the cycle were minimized. Leg orientation during the stance

phase largely determines the ballistic dynamics of the center of mass during aerial phase (Blickhan 1989; McMahon 1990; McMahon and Cheng 1990). The ballistic dynamics are an important contributor to the center of mass position at landing and likely explain the increased IMA for leg orientation during the stance phase.

3.4.2 Co-contraction for leg orientation stabilization

For the task of hopping in place, regardless of target size, leg orientation is over three times more sensitive to changes in shank and thigh angles than to changes in the foot and pelvis angles. This means that for a given amount of angular change in all the joints, errors in shank and thigh angles will translate to the largest deviation of leg orientation. To successfully stabilize leg orientation as task difficulty increases, control of the shank and thigh segment angles, or the knee joint angle, is critical.

Given the increased task demands and the sensitivity of leg orientation to the knee joint angle, to stabilize leg orientation, one strategy might be to stiffen the knee joint through increased co-contraction of muscles across the knee. Since I observed increased stabilization of leg orientation throughout stance, I expected an increase in antagonistic muscle activity across the knee for increased co-contraction. Co-contraction to increase stability of a performance variable during novel tasks has been observed in a variety of studies (Bernstein 1967; Darainy et al. 2004; Darainy and Ostry 2008; Latash and Anson 2006; Woollacott et al. 1988). To test this, I collected EMG data on a subset of my subjects after the initial collection. I found a significant increase in EMG amplitude with task difficulty of all recorded extensor muscles The onset of bursting activity is consistent with EMG recordings from similar muscles in another hopping study (Darainy and Ostry 2008; Hobara et al. 2010; Hobara et al. 2007; Moritz and Farley 2004; Shelburne et al.

2005). Despite the increased activity of LG, MG, VL, VM, and RF muscles, extensor joint torques for all joints did not increase with task difficulty. There was also coactivation of the antagonistic knee flexors muscles MG and LG and knee extensor muscles VL and RF as the period of activation overlapped across all task conditions. In other locomotion tasks where increased knee stabilization is required, a similar co-contraction strategy was observed between the quadriceps and gastrocnemius muscles (Schmitt and Rudolph 2008). The observed co-contraction to increase joint stability can be a compensation strategy in response to difficult or novel tasks.

An alternative explanation for increases in EMG activity of the vasti, rectus femoris, and gastrocnemius muscles may be for mediolateral stabilization. Though the functions of these muscles are typically considered in the sagittal plane, they have also been shown to have significant contributions to frontal plane movements as well (Lawrence et al. 1993a; Pandy et al. 2010). With the current results, it is difficult to determine which, if either, of these explanations is better.

3.4.3 Neural Mechanisms

Increases in lower limb task difficulty have been observed to elicit a neurophysiological response. Specifically, increased cortical activity has been correlated to the need for accurate foot placement. Motor cortex neuronal activity in locomoting cats show significant increases in activity when accurate foot placement is required (Beloozerova et al. 2010; Beloozerova and Sirota 1993a). In human studies, accurate foot placement in a knee extension task resulted in increased cortical activity compared to when accuracy was not required (Wheaton et al. 2007).

The increased cortical activity observed with increases in task difficulty does not always result in increased task performance. I predicted that an increase in segment angle variance to stabilize leg orientation, as seen by my IMA results, would translate to increased task performance. However, I saw no statistical difference in the anterior posterior foot placement variability between targets ($p = 0.08$). In another seat knee extension task, foot placement variability between having a target present and no target was not different despite increases in prefrontal lobe activity (Mizelle et al. 2010a; b; Wheaton et al. 2007). While I could not measure cortical activity directly during this task, I was able to record EMG. The increased EMG activity I saw can be attributed to descending neural drive but can also be from increased gains from reflex pathways or sensory inputs. The exact reasons for the observed increase in EMG activity are not clear and warrant further investigation. However, regardless of the cause of the increase in muscle activity, the increase in activity does result in a proportional increase in signal-dependent motor noise (Harris and Wolpert 1998). The relationship between signal and noise is simply that when the strength of the signal increases, there is a proportional increase in noise. This noise can manifest as motor noise which causes the variance observed in the kinematic outputs. Taken together with the UCM results, the concomitant increase in EMG activity and IMA suggests that when task difficulty increases such that the neuromuscular system responds with increased co-contraction, the additional variance due to the increased noise is structured toward stabilizing performance variables.

3.4.4 Implications on novel, difficult tasks

There is a significant negative correlation between leg orientation and leg length IMA as task difficulty increases, which suggests that there is a trade-off effect between

stabilization of leg orientation and leg length (Figure 3.5**)**. Further analysis revealed that the task spaces for leg orientation and leg length stabilization were at an orientation of 78^{o}-85^{o} relative to each other throughout the hopping cycle. Consequently, the GEV component for leg length largely occupies the NGEV space of leg orientation and vice versa. Although the spaces are orthogonal, this does not mean the two variables cannot be simultaneously stabilized as there exists a solution space where the two task spaces intersect. It is in this intersection where the solution space will allow for simultaneous stabilization of both leg orientation and leg length. This is in fact exemplified at mid-stance when hopping in the small target condition (Figure 3.3c & f). In terms of limb control, one strategy is to simultaneously control all performance variables throughout the entire task, e.g. this type of control has been implemented in robotic systems (Khatib 1987; Khatib et al. 2004). Alternatively, my results suggest that biological systems prefer to maximize the solution space by only stabilizing performance variables at times that are critical to each task (Auyang et al. 2009; Yen and Chang 2009). Like robotic systems, humans are capable of stabilizing both leg orientation and leg length simultaneously; however, they do not choose to do so unless the task requires it. This supports the idea that the neuromuscular system favors a "control as needed" strategy to maximize redundancy rather than a "control always" strategy. A similar result has been show in vertical and horizontal force control during hopping (Yen and Chang 2009). Maximizing motor redundancy in this way may be a strategy for allowing the locomotor system to be more adaptable to different tasks. However, this may be a strategy specific to relatively novel tasks. Studies have shown that performers of skilled, practiced tasks show decreased total variance of local variables (Halliday et al. 1995). With time and practice

of a task, we may learn to minimize task variance and noise to perform the task better and rely less on structuring variance. The ability to structure variance allows us to better compensate for new perturbations and disturbances that may arise making us more robust to changing conditions. In the event of an over trained, precision task, the task demands may require such a high number of task constraints that there is little to no motor redundancy present to compensate for perturbations.

3.5 Conclusions

Segment angle variance was increasingly structured to stabilize leg orientation as target size decreased. Decreasing the target size increased the task difficulty and the importance of leg orientation for task completion. There was a significant decrease in leg length stabilization as task difficulty increased. Despite being able to simultaneously stabilize both leg orientation and leg length as seen during midstance, both performance variables were not simultaneously stabilized throughout most of the hopping cycle. This suggests that humans try to maximize solution space during locomotion and only stabilize leg orientation and leg length at times when they are critical to task completion. The increase in activity of antagonistic knee muscles with task difficulty coincided with the increase in total segment angle variance. This variance was increasingly structured to stabilize leg orientation with increased target difficulty. This suggests that increased central drive or reflex gains could be the source of the increased variance that required additional structuring. Maximizing the operation space provides the neuromuscular system with the ability to compensate for changes in locomotor task difficulty.

CHAPTER 4

EFFECT OF MULTIPLE TASK CONSTRAINTS ON LEG LENGTH AND LEG ORIENTATION STABILIZATION STRATEGIES

4.1 Introduction

Locomotion is one of the most common motor tasks performed on a daily basis. Yet, the locomotor system is constantly affected by external perturbations and task demands. Despite this, the human body is able to adapt quickly and effectively to these perturbations to maintain stable, cyclical, gait.

One of the reasons the human body is capable of rapid compensations to perturbations during locomotion is because of the kinematic motor redundancy of the lower limbs. The control of such a complex, kinematically redundant system is a major topic in the field of motor control. Recent research has shown that during a simple locomotion task such as hopping in place, the neuromuscular system achieves stable hopping dynamics by stabilizing key performance variables, such as leg length, leg orientation, or end point forces (Auyang et al. 2009; Yen et al. 2009; Yen and Chang 2010). The term "stabilizing" is used to mean minimizing the cycle to cycle variance of a given performance variable. Stabilization of these performance variables are quantified using an Uncontrolled Manifold (UCM) analysis. This analysis determines how the variance of local variables, such as joint angles, is structured to stabilize the hypothesized performance variable (Auyang et al. 2009; Scholz and Schöner 1999; Yen et al. 2009; Yen and Chang 2010). The use of leg orientation and leg length as performance variables during locomotion is supported by many different areas of research including

computational neuroscience, biomechanics, robotics and neurophysiology (Blickhan 1989; Bosco and Poppele 2000; Bosco et al. 2000; Chang et al. 2009; Ivanenko et al. 2007; Ivanenko et al. 2008; Lacquaniti et al. 1990b; McMahon and Cheng 1990). Hopping in place as a locomotion model has provided valuable insight into how leg orientation and leg length are stabilized across a variety of conditions such as non-preferred frequencies and accurate foot placement (Auyang et al. 2009). Leg orientation is stabilized in aerial phase and leg length is stabilized during mid-stance, regardless of changes due to task difficulties (Auyang et al. 2009). However, hopping in place lacks a fundamental characteristic found in everyday locomotion: forward velocity. This study will seek to quantify leg orientation and leg length stabilization strategies within the context of forward human hopping.

A one legged forward human hopping model is the logical progression from hopping in place in regards to studying how segment angles are coordinated to stabilize leg orientation or leg length. Unlike running, the more common human bouncing gait, one legged forward hopping is not affected by the complex interactions between the swing-leg and stance-leg (Blum et al. 2010; Knuesel et al. 2005; Seyfarth et al. 2003). Forward human hopping will provide needed insight into how the forward component of locomotion affects leg orientation or leg length stabilization strategies, if at all. While hopping in place and forward hopping are similar tasks, the forward velocity component does add several considerations that may affect leg orientation and leg length stabilization strategies. For a sagittal plane analysis, hopping in place is predominantly a one-dimensional task while the forward velocity component of forward hopping adds a second dimension to the task. Where as in hopping in place, the center of mass was

mostly over the base of support, during forward hopping, the center of mass is rarely over the base of support which may affect balance and leg orientations stabilization needs. While achieving a certain leg length during aerial phase of hopping in place was not important, in forward locomotion toe clearance during the "swing" phase may require more control of leg length (Moosabhoy and Gard 2006; Virji-Babul and Brown 2004). These are just some examples of the different task needs that may change leg orientation or leg length stabilization during the hopping cycle as a result of adding a forward velocity component.

In addition to identifying differences in leg orientation or leg length stabilization strategies due to an added forward velocity constraint, I will also test how leg orientation and leg length stabilization changes in response to changes in task difficulty. A number of studies with a variety of tasks have shown that increased task difficulty results in increases in local variable variance being structured to stabilize a performance variable. When subjects were asked to hop into smaller target sizes, more segment angle variance structured to stabilize leg orientation (Chapter 3). There is a consistent trend between increased task difficulty and the resulting increased variance being structured to stabilize the constrained performance variable. To further test this trend in the context of forward locomotion, I will have subjects hop forward at a constant speed and land into different sized landing areas projected onto the floor of the treadmill. Since the relationship between decreasing target size and the stabilization of leg orientation and leg length has been quantified in a previous study (Chapter 3), any changes in that relationship will be due solely to the forward velocity component.

The purpose of this study is to quantify leg orientation and leg length stabilization strategies during forward hopping. I hypothesize that the characteristic periods during the hopping in place cycle that leg orientation and leg length are stabilized, aerial phase and mid stance respectively, will also be stabilized during forward hopping. Due to the need for minimum toe clearance during the swing phase, I also hypothesize that leg length will be additionally stabilized during swing. Finally, I hypothesize that as task difficulty increases through decreased landing area size, average leg orientation stabilization should increase with no change to leg length stabilization.

4.2 Methods

4.2.1 Subjects

Eleven healthy human subjects with no prior history of lower extremity injuries volunteered for this study (6 males, 5 females, mean (SD) age = 27(5) years, mass = 60.5(10.1) kg). All subjects gave informed consent prior to participating in this study as approved by the Georgia Institute of Technology's Human Subjects Institutional Review Board.

4.2.2 Experimental Protocol

I made anatomical measurements and placed eight retroreflective markers on anatomical landmarks on each of the lower extremities using a modified Helen Hayes marker set (anterior superior iliac spine, posterior superior iliac spine, thigh segment, lateral femoral epicondyle, shank segment, lateral malleolus, head of the second metatarsal phalangeal joint, and calcaneus). Subjects hopped forward on a treadmill at a speed of 0.8 m/s on one-leg at 2.2Hz for three trials per target condition (large, medium,

and small). Targets were projected onto the treadmill from a projector positioned in front and above the subjects. Hopping frequency was determined based on previously reported preferred hopping frequencies (Farley et al. 1991). Forward speed was based on the average comfortable speeds of three pilot subjects of varying height and mass. The order of the target conditions was randomized for each subject. Subjects matched the prescribed hopping frequency to the beat of an audible metronome, with a minimum of thirty-second practice period to become familiar with hopping at the prescribed frequency, speed, and target conditions. Each data collection trial lasted approximately thirty seconds. Subjects hopped on their right leg. Approximately 190 hops were analyzed per subject per target condition.

4.2.3 Target Sizes

I used three target sizes to vary task difficulty. The size of each target was calculated based on desired Index of Difficulty (ID) and Fitts' law, a logarithmic relation between the ratio of twice the travel distance and the target width (Fitts 1954; Fitts and Peterson 1964). From a previous study, I determined the travel distance as the average maximum toe height from the ground for hopping in place at 2.2Hz (Auyang et al. 2009). I chose a linear increase in ID: .25 (easiest), .50, and 1.0 (most difficult). The resulting target sizes were .25m^2, .063m^2, and .010m^2, respectively.

4.2.4 Kinematics and Kinetics

I used a five camera motion-analysis system (120Hz; Vicon Motion Systems; Los Angeles, CA) to capture kinematic marker data. I filtered data using a zero phase shift fourth-order Butterworth low-pass filter with a 10Hz cut-off frequency. I calculated four sagittal plane segment angles (foot, shank, thigh, pelvis) with respect to horizontal with

software coded in Matlab (Mathworks, Natick, MA) using the toe and anterior superior iliac spine (ASIS) marker positions and the calculated ankle, knee, and hip joint centers to create a linked segment kinematic model. I determined ground contact and liftoff events using a force platform (1080 Hz; AMTI; Watertown, MA) by detecting when the vertical ground reaction force crossed a threshold of 32 N.

4.2.5 Uncontrolled Manifold Analysis

An Uncontrolled Manifold analysis was used to quantify whether segment angle variance was purposefully structured to stabilize leg orientation or leg length from cycle to cycle variance. Specifics of this analysis can be found in Section 2.2.4.

4.2.6 Electromyography

I did a post-hoc collection of electromyography (EMG) data from five of my original subjects. The protocol was repeated as described earlier with the collection of EMG from seven muscles of the right leg: tibialis anterior (TA), lateral gastrocnemius (LG), medial gastrocnemius (MG), vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), and the long head of the biceps femoris (BF). Data were collected using a wireless EMG system (1080Hz, Noraxon TeleMyo 2400T G2). EMG data were band pass filtered from 10-500Hz, rectified, and low pass filtered at 10Hz. EMG data for each channel were normalized to the peak activity recorded during the large hopping condition for that channel. Burst duration and amplitude were calculated for each muscle

4.2.7 Statistical Analysis

A Student's one sample t-test ($\alpha = 0.05$) was used to test whether normalized total variance of segment angles changed with target difficulty. The same test ($\alpha = 0.05$) was

used to test for significant differences in normalized leg orientation or leg length GEV and NGEV with target difficulty. To determine whether a performance variable was stabilized by local variables, I performed a Student's one-sample, two-tailed t-test ($\alpha = 0.05$) to test whether IMA was significantly different than zero. To test whether target size caused changes in IMA, I used a repeated measures analysis of variance (ANOVA) to test for interaction effects of average IMA across time and target size ($\alpha = 0.05$) and a post-hoc test with Bonferroni correction to determine which targets had different IMAs. I used a repeated measures analysis of variance (ANOVA) to test for the effect of target size on mean EMG activity and EMG burst duration. All statistical analyses were done using SPSS software (SPSS Inc.; Chicago, IL).

4.3 Results

4.3.1 Task Performance

The average anterior posterior and mediolateral foot placement range was not statistically different between the three target sizes during forward hopping (Table 4.1, Figure 4.1b). The average anterior posterior and mediolateral foot placement range for hopping in place is also presented here. There were no statistical differences between the average anterior posterior and mediolateral foot placement range for all three target sizes during forward hopping and the small target during hopping in place. Average hopping frequency for each subject showed no difference compared to the prescribed frequency of 2.2Hz and no difference with changes in target (Table 4.1). Step length, defined as the distance from the point of take off to the point of contact showed no statistical difference (Table 4.1).

Table 4.1 Mean hop parameters and foot placement variability. Average and standard deviations of hopping parameters for three target conditions at both hopping in place and forward velocity. Average and standard deviations for foot placement range of 95% confidence interval of the hops about the center of landing distribution in both medial and lateral directions are presented as well.

	Large		Medium		Small	
n = 11	0 m/s	.8 m/s	0 m/s	.8 m/s	0 m/s	.8 m/s
Step length (m)	0(.037)	.1991(.0071)	0(.031)	.2011(.009)	0(.026)	.2045(.0095)
Frequency (Hz)	2.17(.001)	2.15(.002)	2.18(.001)	2.18(.001)	2.16(.001)	2.15(.002)
Anterior posterior foot placement range (m)	.185(.0382)	.183(.0327)	.187(.0364)	.181(.0315)	.182 (.0347)	.179(.0320)
Mediolateral foot placement range (m)	.191(.0484)	.133(.0194)	.163(.0375)	.128(.0228)	.127(.0221)	.129(.0284)

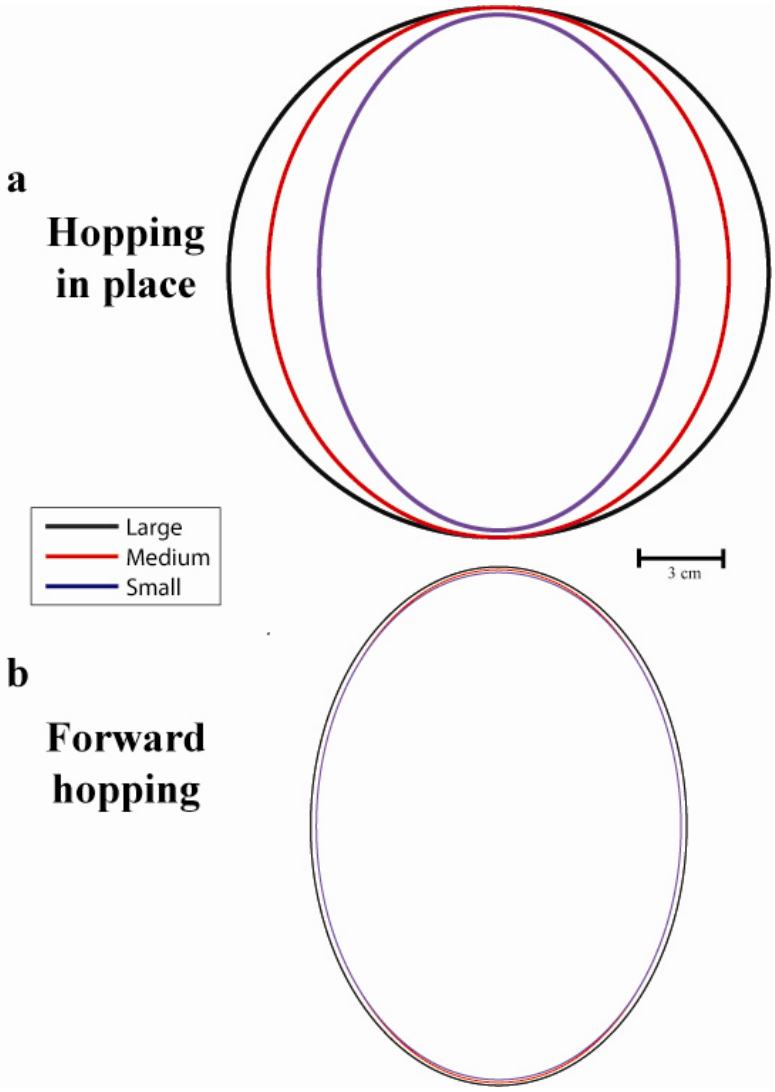

Figure 4.1 Distribution of landing positions.
95% confidence interval of the landing positions for a) hopping in place and b) forward hopping for large (black), medium (red), and small (blue) targets. Data for hopping in place is taken from previous study (Chapter 3). There were no statistical differences between any of the distributions between targets in forward hopping or with that of the small target during hopping in place.

4.3.2 UCM Results

Total segment angle variance relative to the large target condition was calculated for the medium and small target conditions (n = 11). Total segment angle variance did not change as the target size got smaller (p=0.53, Figure 4.2). The GEV and NGEV components relative to the large target condition were calculated for leg orientation and leg length in the medium and small target conditions (n = 11, Figure 4.3). There were no changes in the GEV or NGEV components for leg length or orientation (p=0.47).

IMA allows us to analyze the relationship between GEV and NGEV across subjects. In the large target condition, leg orientation IMA showed significant destabilization for half of stance (10-60% of stance) and significant stabilization for most of aerial phase (1-70% of aerial phase; $p \leq 0.01$, Figure 4.4a). In the medium target condition, leg orientation IMA showed significant destabilization throughout most of stance (10-70% of stance) and significant stabilization throughout most of aerial phase (1-80% of aerial phase; $p \leq 0.01$, Figure 4.4b). In the small target condition, leg orientation IMA showed significant destabilization throughout most of stance (10-80% of stance) and significant stabilization throughout most of aerial phase (1-80% of aerial phase; $p \leq 0.01$, Figure 4.4c). For all target conditions, peak destabilization occurred at midstance while peak stabilization occurred in the middle of aerial phase ($p \leq 0.01$). Average leg orientation IMA for all target conditions showed no statistical difference from zero ($p > 0.05$) and did not change with target conditions ($p > 0.05$, Figure 4.5).

In the large target condition, leg length IMA showed significant stabilization during 10-80% of stance and 1-90% of aerial phase ($p \leq 0.01$, Figure 4.4d). In the medium

target condition, leg length IMA showed significant stabilization throughout the hopping cycle

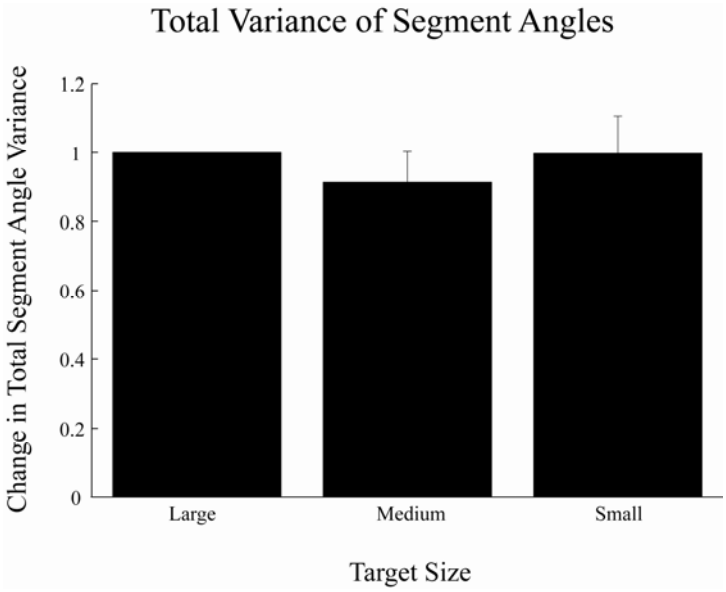

Figure 4.2 Total segment angle variance normalized to large target condition. Bars are the averaged total variances for all subjects with ±1 standard deviation. Total segment angle variance did not change as target size decreased.

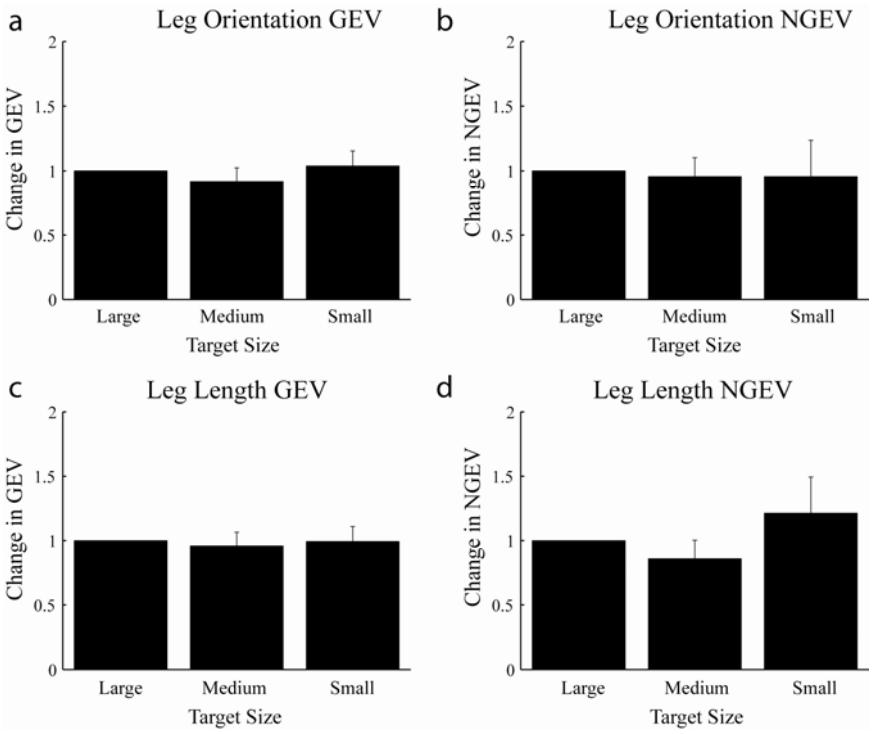

Figure 4.3 Goal equivalent variance (GEV) and non-goal equivalent variance (NGEV) Goal equivalent variance (GEV) and non-goal equivalent variance (NGEV) normalized to large target condition for the three target conditions for (**a** & **b**) leg orientation and (**c** & **d**) leg length. Bars are the averaged total variances for all subjects with ±1 standard deviation. Neither leg length or leg orientation GEV or NGEV components changed with target sizes.

($p \leq 0.01$, Figure 4.4e). In the small target condition, leg length IMA showed significant stabilization throughout most of the hopping cycle ($p \leq 0.01$, Figure 4.4f). For all target conditions, in stance phase, peak stabilization occurred at midstance ($p \leq 0.01$). For all target conditions, in the aerial phase, peak stabilization occurred during the middle of aerial phase ($p \leq 0.01$). Average leg length IMA for all target conditions was greater than zero ($p \leq 0.01$) and did not change with target conditions ($p > 0.05$, Figure 4.5).

An analysis of the orientation of the leg orientation manifold vs. the orientation of the leg length manifold revealed that the manifolds are highly orthogonal to each other at an average of $83^{o} \pm 2^{o}$ throughout the entire hopping cycle.

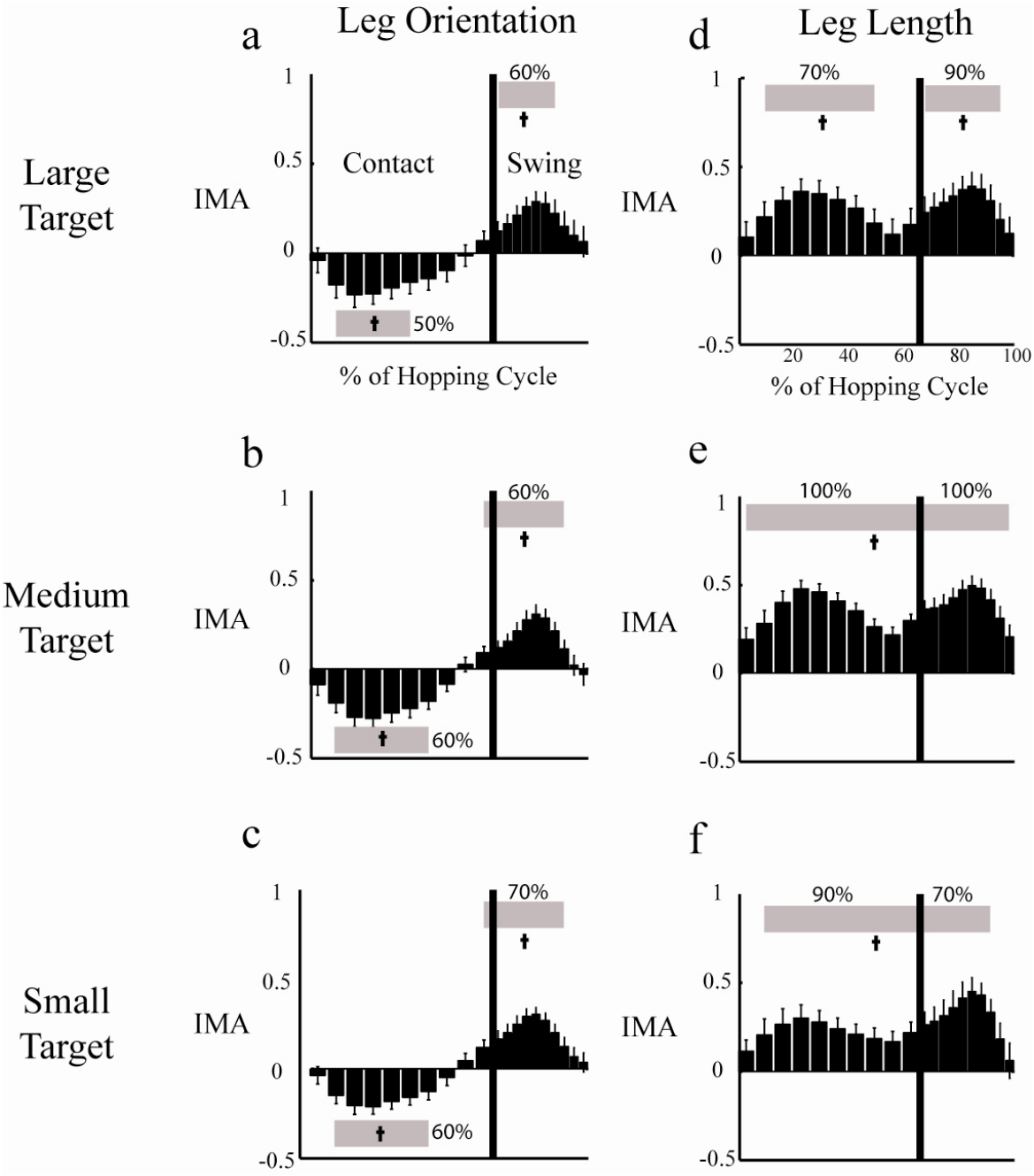

Figure 4.4 Index of Motor Abundance (IMA)

Index of Motor Abundance (IMA) **(a-c)** for leg orientation stabilization across three target conditions and **(d-f)** leg length stabilization across three target conditions. Bars are the averaged IMA for 10% intervals in contact and aerial phase (n = 11) with ±1 standard deviation. Leg orientation was destabilized during the period around midstance and stabilized around the middle of swing phase. There was no change with target sizes. Leg length showed maximum stabilization around midstance and middle of aerial phase for all target sizes. Gray bar denotes period where IMA was significantly different than 0 ($p<0.01$). Horizontal grey line above the bins if IMA is greater than zero and below the bins if IMA is less than zero.

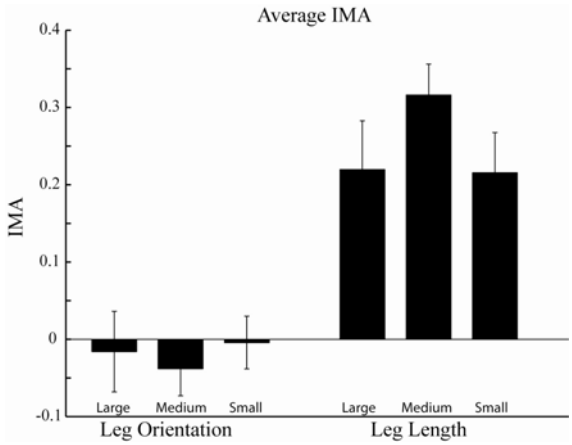

Figure 4.5 Average Index of Motor Abundance (IMA)
Average Index of Motor Abundance (IMA) for leg orientation and leg length for the three target conditions. Bars are the averaged IMA for all subjects and bins with ±1 standard deviation. Average leg orientation IMA did not change with target difficulty. Average leg length IMA did not change with target difficulty.

4.3.3 EMG

EMG data were collected from five of the eleven subjects in a separate pos-hoc collection. There were no significant differences in mean EMG activity during stance or swing phase for any muscles with increased difficulty (Figure 4.6a-b, $p>0.05$). There were also no significant differences in duration of EMG bursting activity in swing or aerial phase (Figure 4.6c-d, $p>0.05$).

4.3.4 Hopping in place

Results for hopping in place are published in a previous study (Chapter 3). For the purposes of discussion, certain data are reproduced here to better illustrate similarities and differences in performance and stabilization strategies of leg orientation and leg length observed in forward hopping and hopping in place (Table 4.1, Figure 4.1).

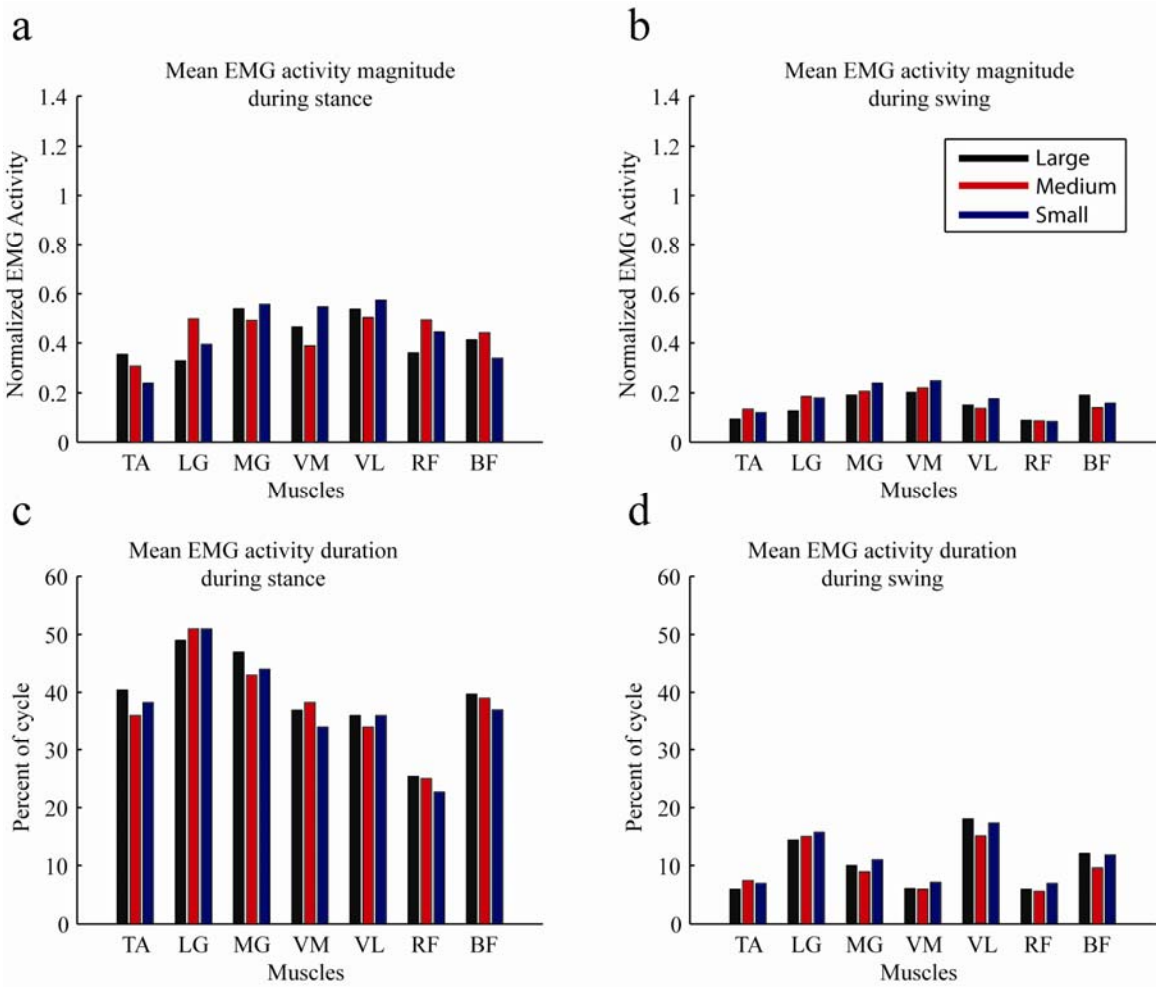

Figure 4.6 Average burst EMG activity and burst duration.
Average EMG activity of recorded muscles in (**a**) stance phase and (**b**) swing phase showed no change across the three target conditions. Average EMG activity duration of recorded muscles in (**c**) stance phase and (d) swing phase showed no change across the three target conditions.

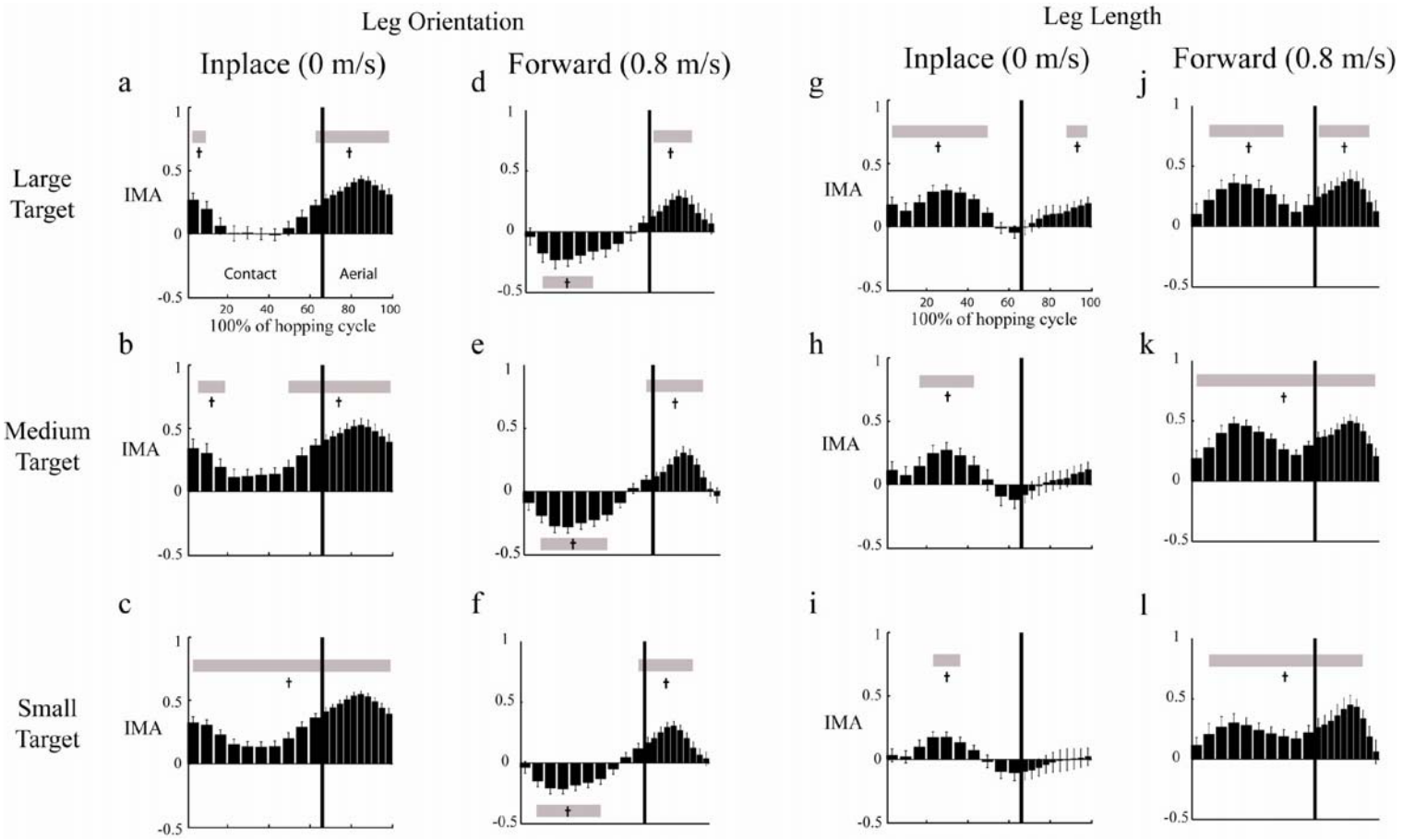

Figure 4.7 Leg orientation and leg length IMA data

Leg orientation and leg length IMA data for (**a-f**) leg orientation and (**g-l**) leg length for three target conditions for hopping in place and forward hopping. Leg orientation IMA was stabilized in aerial phase at both speeds for all target conditions. Unlike leg orientation IMA during hopping in place, leg orientation was destabilized at midstance during the forward hopping condition and did not change with target conditions. Leg length was stabilized at midstance at both speeds for all target conditions. Unlike leg length IMA during hopping in place, leg length was stabilized in aerial phase during the forward hopping condition and did not change with target conditions.

4.4 Discussion

The purpose of this study is to investigate the effects of increases in task difficulties coupled with forward velocity on leg length or leg orientation stabilization strategies. Previous findings showed that during hopping in place, increases in task difficulty through constraining the target landing area resulted in increases in segment angle variance being structured to stabilize leg orientation. I hypothesized that leg orientation and leg length would see peak stabilization at mid-aerial and mid-stance respectively. I also hypothesized that the forward movement constraint would require leg length to be stabilized in aerial phase. Finally, as was the case for previous findings, I hypothesized that leg orientation stabilization would increase with task difficulty. I found that leg length stabilization did show significant stabilization during aerial phase. Leg orientation stabilization did not increase with increase in task difficulty has I had predicted.

4.4.1 Leg orientation and leg length stabilization in forward hopping

As I hypothesized, leg orientation IMA shows the characteristic peak in the middle of aerial phase (Figure 4.4a-c) and leg length IMA showed a characteristic peak at midstance (Figure 4.4d-f), consistent with previous findings (Auyang et al. 2009), Chapter 3). Leg orientation stabilization in aerial phase is important for achieving specific forward velocities (Blickhan 1989; McMahon and Cheng 1990; Raibert et al. 1984). Leg length is important at midstance because the leg is in its most flexed posture, small deviations in segment angles will result in larger than normal deviations in leg length (Auyang et al. 2009). Peak forces are also seen at midstance (Farley et al. 1991) and stabilization of leg length may be to limit peak joint moments. The characteristic

peaks of leg orientation IMA in the middle of aerial phase and leg length at midstance shows the importance of stabilizing these two variables at their respective times in the hopping cycle, even for different hopping tasks.

A unique IMA characteristic of forward hopping is the significant destabilization of leg orientation seen in midstance (Figure 4.4a-c). While this period of the cycle has been typically characterized by a low IMA during hopping, it has never shown significant destabilization, i.e. IMA less than zero (Auyang et al. 2009). The purposeful destabilization of a performance variable is necessary when the value of a performance variable needs to be changed quickly or when stabilization strategy changes (Shim et al. 2005). One possible explanation is that leg orientation is destabilized in order for another performance variable to change, such as horizontal force. Unlike hopping in place, the horizontal force profile of forward hopping has a distinct braking component followed by a propulsive component (Blickhan 1989; McMahon and Cheng 1990). Because the horizontal component of the ground reaction force is largely dependent on leg orientation, leg orientation may be destabilized in order to change from a braking horizontal force strategy to a propulsive horizontal force strategy. Another possibility is that the destabilization of leg orientation is for the stabilization of leg length. The leg orientation and leg length UCMs are approximately orthogonal to each other. As seen in previous study, when two performance variables have orthogonal UCMs, often, one variable is prioritized at the expense of stabilizing the other (Latash et al. 2001; Yen and Chang 2009). The results of the current study could be a case where leg length requires such high stabilization that leg orientation is simply pushed to being destabilized. Further

investigation is required to determine whether the destabilization of leg orientation is purposeful or if it is simply the trade off from having to stabilize leg length.

Another unique IMA characteristic in forward hopping is the leg length stabilization in the aerial phase that is not seen during hopping in place. Leg length has significant importance in forward hopping that is not seen in the special case of hopping in place: toe clearance. The minimum limit of toe position during swing is defined by the minimum height of the toe needed to clear any obstacles and not trip (Moosabhoy and Gard 2006; Virji-Babul and Brown 2004). The upper limit of toe position during swing is probably due to a minimization of energetic costs (Detrembleur et al. 2005; Gordon et al. 2009). An invariable leg length trajectory must be achieved during swing in order to satisfy both of these implicit task constraints.

4.4.2 Effect of target sizes and velocity

Task difficulty was adjusted by changing the target sizes of the landing area. When hopping forward at 0.8m/s, decreasing the target size yielded little to no change in either leg orientation or leg length IMA across the entire hopping cycle (Figure 4.4). Average leg orientation IMA showed no statistical change with target size nor was it statistically different than zero at any target conditions (Figure 4.5). Average leg length IMA also showed no statistical change with target sizes but was statistically greater than zero for all target conditions (Figure 4.5). These results are inconsistent with previous findings for hopping in place with changing task difficulties (Auyang et al. 2009). The results from the hopping in place study showed increased average leg orientation IMA as target size decreased and IMA was always greater than zero. Since the only difference

between the two studies was the inclusion of the forward velocity component, differences in IMA results are likely to be due to the effects of the forward velocity constraint.

Despite changes in task difficulty, decreasing target sizes did not seem to have an effect on leg length or leg orientation stabilization or overall landing performance. The distribution of anterior posterior foot placement was not different between all target conditions during either hopping in place or forward hopping (Table 4.1, Figure 4.1). The mediolateral distribution of foot placement was not different between target conditions during forward hopping and not different compared to hopping in place into the small target (Table 4.1, Figure 4.1). In short, anterior posterior and mediolateral foot placement performance for all targets during forward hopping was not different compared to hopping in place into the small target. However, in forward hopping, subjects were able to achieve the same level of performance without any changes in leg orientation IMA as seen during hopping in place. Two points need to be considered here. First, how is anterior posterior performance achieved and second, how is mediolateral performance achieved.

In forward locomotion, accurate anterior posterior foot placement has been shown to be largely dependent on step length (Hodgins and Raibert 1991). In the present study, step length had very low variability (Table 4.1) which suggests it was also stabilized from cycle to cycle. Step length may be a higher order performance variable that the neuromechanical system stabilizes during locomotion for accurate foot placement. By stabilizing step length from cycle to cycle, subjects would be able to reproducibly place their foot accurately. Step length can be defined as follows (Figure 4.7, Eq. 4.1):

$$\text{Step length} = (X - X_o) + L_{off}*\cos(\theta_{off}) + L_{contact}*\cos(\theta_{contact}) \quad (4.1)$$

where X_o is the horizontal position of the center of mass at toe off, X is the horizontal position of the center of mass at contact, L_{off} and $L_{contact}$ are the leg lengths at toe off and contact respectively, and θ_{off} and $\theta_{contact}$ are the leg orientations at toe off and contact respectively. Since step length is dependent on both the stabilization of leg length and leg orientation, step length may be a higher order performance variable that is stabilized through structuring leg length and leg orientation variance (Figure 4.8). It is outside of the scope of this project to test for the purposeful structure of leg length and leg orientation variance. However, future studies and analysis should further explore this potential hierarchy.

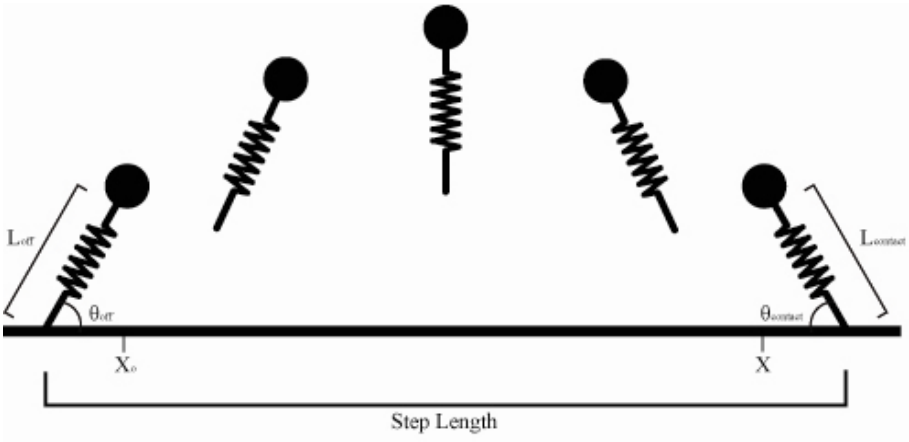

Figure 4.7 Step length model
Sagittal plane spring-mass model and variables to illustrate step length definition. X and X_o are the positions of the horizontal position of the center of mass at foot contact and toe off respectively. $L_{contact}$ and L_{off} are the leg lengths at foot contact and toe off respectively. $\Theta_{contact}$ and θ_{off} are the leg orientations at foot contact and toe off respectively.

While the UCM analysis of this study was done purely in the sagittal plane, other metrics such as EMG and foot placement performance takes into account the frontal plane as well. One proposed reason for the increase in leg orientation IMA during hopping in place in smaller targets was because there was increased co-contraction of muscles across the knee to stabilize leg orientation, as reflected by the increase in EMG activity of those

muscles (Chapter 3). This increase in activity resulted in a concurrent increase in noise which can manifest as kinematic variance (Faisal et al. 2008; Harris and Wolpert 1998; Stein et al. 2005). This additional variance needs to be structured such that leg orientation stabilization was not affected, hence increased IMA. I believe that the increase in muscle activity may have been to stabilize the mediolateral component of leg orientation. Recent work has shown that the vasti and gastrocnemius muscles of the lower limb function in both sagittal and frontal planes during human locomotion (Pandy et al. 2010). In the frontal plane, these muscles provide mediolateral stability. The observed increase in muscle activity during hopping in place with smaller targets may be to provide mediolateral stability during walking. This is supported by the decrease in mediolateral distribution of foot placement observed during hopping in place with smaller targets (Table 4.1, Figure 4.1a). In the present study, there was no change in EMG activity of recorded muscles and no change in the mediolateral distribution of foot placement compared to what was seen during the most difficulty hopping in place condition with the small target (Figure 4.1, 4.6, Table 4.1). Mediolateral stability may be achieved through the dynamics of the task requirements. Mediolateral sway of the center of mass decreases with increases in forward speed (Orendurff et al. 2004). Because mediolateral foot placement is passively stabilized, there is no increase in EMG activity and therefore no increased noise that needs to be structured to stabilize leg orientation. The fact that anterior posterior foot placement performance does not change with any condition and mediolateral foot placement performance does not improve beyond what is seen in the forward condition or the smallest target in the hopping in place condition suggest a

functional limit in regards to how well subjects are able to minimize variability in these directions.

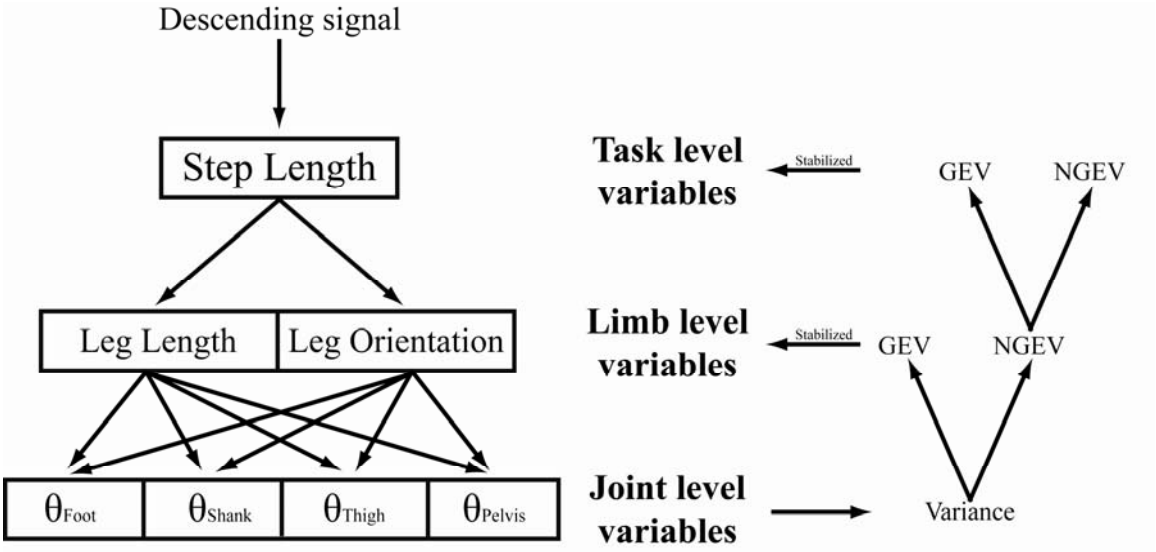

Figure 4.8 Proposed hierarchical control and variance of variables during locomotion
A proposed hierarchy of three different levels of variables: task level, limb level, and joint level variables. Variables listed here are only those that were investigated and described in this work and is not intended to suggest that these are the only variables at each level as there are surely more. Also shown is how the variance of each level translates up the hierarchy. At the lowest level of this proposed hierarchy, segment angle variance is structured into GEV and NGEV. From here, only the NGEV of limb level variables are translated up to the task level.

4.4.3 Special case of hopping in place

While the UCM results for leg orientation and leg length stabilization in the current study appear to contradict those found during hopping in place with different targets, the proposed hierarchy of performance variables can reconcile the two results to some extent (Figure 4.8). Hopping in place is a special case where θ_{off} and $\theta_{contact}$ ~=90^o. Because the cos(90^o) is 0, as long as θ_{off} and $\theta_{contact}$ are stabilized such that they are approximately 90^o, the terms L_{off}*cos(θ_{off}) and $L_{contact}$*cos($\theta_{contact}$) from Eq. 4.1 both approach 0, regardless of changes to L_{off} or $L_{contact}$,. In short, during hopping in place, the L_{off}*cos(θ_{off}) and $L_{contact}$*cos($\theta_{contact}$) terms of step length are dependent entirely on leg

orientation. Consequently, in the special case of hopping in place, stabilizing leg orientation is sufficient to stabilize two of the terms that define step length.

4.4.4 Advantages of hierarchical organization of performance variables

Stabilization of step length can be achieved by decreasing the variance of elements that contribute to it, i.e. leg length and leg orientation, or by structuring leg orientation and leg length variance. Because of the orthogonality of the leg orientation and leg length task spaces, to decrease variance in both leg length and leg orientation would require operating in the intersecting space of those manifolds. Operating in the intersecting space would greatly reduce the operational space available to the locomotor system. Instead, through structuring leg orientation and leg length variance, step length can still be stabilized from cycle to cycle while maintaining more motor redundancy. From my IMA results, the previous statement may seem contradictory as I see that both leg orientation and leg length are not stabilized at takeoff and contact. When considering a performance variable hierarchy in the context of a UCM analysis, we have to consider the variance that is being structured as we move up the hierarchy (Figure 4.8). The GEV components of segment angle variance go to making leg length or leg orientation invariant while the NGEV component directly creates error or variance in the performance variable that is observed from cycle to cycle. It is the NGEV components from lower level performance variables that migrate up the hierarchy. The combined variance of leg orientation and leg length due to their respective NGEV components can then be further structured to stabilize higher order performance variables like step length. As step length is dependent on leg orientation and leg length at takeoff and contact, only stabilization of leg orientation and leg length around these time points should be critical

to achieving the desired step length. Takeoff and contact are where I see the highest NGEV:GEV ratios in leg length IMA. These points are not the highest NGEV:GEV in leg orientation, but still show little to no stabilization. Because leg orientation and leg length are both important to stabilizing step length, the locomotor system maintains some variance in both these variables at these time points to stabilize step length.

4.5 Conclusions

While the stabilization strategies of leg orientation and leg length during forward one-legged hopping showed similarities with those seen during hopping in place, there were significant differences due to forward progression. The characteristic peak stabilization of leg orientation during aerial phase and leg length at midstance for hopping in place were still present but leg orientation also showed a new peak of destabilization at midstance and leg length showed a second peak in stabilization in aerial phase. The forward velocity constraint added additional task demands such as toe clearance that required leg length stabilization in aerial phase. Unlike previous studies, changes in task difficulty did not result in any change in leg orientation or leg length stabilization. Accurate anterior posterior foot placement in forward locomotion is dependent on stabilizing a higher order performance variable step length that is a function of both leg length and leg orientation.

CHAPTER 5

CONCLUSIONS

Human locomotion is incredibly robust. It is capable of rapidly adapting to obstacles and perturbations in a variety of locomotor tasks. One resource that allows for this is the motor redundancy of the human body. Control of a complex, kinematically redundant system such as the human body has been an important topic of motor control. The aim of this dissertation is to gain a better understanding of how kinematic motor redundancy is utilized to stabilize the performance variables leg length and leg orientation during human locomotion. In this chapter, I will review the major findings of this dissertation and discuss the implications of these results on motor control and locomotion.

5.1 Major findings

The first aim of this dissertation was to ascertain whether the variance of segment angles is purposefully structured such that the cycle to cycle variance of leg length or leg orientation is minimized during the locomotion task of hopping in place. To test this, I used an Uncontrolled Manifold (UCM) analysis. This analysis partitions segment angle variance into two categories: variance that does not change the performance variables or goal equivalent variance (GEV) and variance that changes the performance variables or non-goal equivalent variance (NGEV). I used a metric called the Index of Motor Abundance (IMA) that describes the relationship of GEV and NGEV. IMA values greater than zero mean that segment angle variance has a non-random, purposeful structure that stabilizes leg length or leg orientation from cycle to cycle deviations. An IMA of zero

means that there is no purposeful structure to the segment angle variance. Finally, an IMA less than zero means that segment angle variance has a non-random, purposeful structure to destabilize leg length or leg orientation.

5.1.1 Leg length and leg orientation as performance variables

Based on the spring-mass model for hopping, I tested leg length and leg orientation as two possible kinematic performance variables during human hopping in place. At 2.2Hz (approximately preferred frequency for humans) hopping, leg length and leg orientation are in fact performance variables that are stabilized from cycle to cycle through the purposeful structuring of segment angle variance (**Chapter 2**). Interestingly, leg length and leg orientation are not stabilized throughout the entire hopping cycle as I had initially hypothesized. Instead, leg length IMA is highest at midstance phase while leg orientation IMA peaks in mid-aerial phase (Figure 2.5). These two peaks are characteristic of leg length and leg orientation stabilization across many hopping conditions.

5.1.2 Effects of task constraints during hopping in place

My second aim was to test how robust the leg length and leg orientation stabilization strategies discovered during preferred frequency hopping in place were with different task conditions and constraints (**Chapter 2**). The first task constraint was hopping at higher, non-preferred frequencies (2.8Hz and 3.2Hz). As subjects hop at higher frequencies, leg length IMA increases throughout the cycle except at the characteristic midstance peak where it persisted at the same magnitude. Leg orientation IMA shows little to no change with frequency across the hopping cycle (Figure 3.3). Stabilizing leg length at higher frequencies appears to be more important than stabilizing

leg orientation. This is likely because for hopping in place, the hopping frequency is dependent on leg length and not leg orientation stabilization (Eq. 2.10).

My second experimental constraint was limiting the target landing area during hopping in place (**Chapter 3**). In terms of IMA results, hopping in the large target is not any different than hopping without a target present (Figure 2.5 a & d and 3.3a & d). As the target sizes got smaller and task difficulty increases, leg orientation IMA increases across the rest of the hopping cycle approaching the magnitude of the characteristic peak in mid-aerial phase. In contrast, leg length IMA decreases throughout the cycle as target size decreases (Figure 3.3). Despite this overall decrease, leg length IMA is still greater than zero and peaks at midstance. This tradeoff between leg length and leg orientation stabilization can be largely explained by the orientation of their respective UCMs. The leg length and leg orientation UCMs are approximately orthogonal during hopping in place. Therefore, most combinations of segment angles that stabilize one will destabilize the other. Notably, it is possible to simultaneously stabilize both, as seen during midstance of hopping in the smallest target (Figure 3.3). This situation reflects a set of solutions that exists in the intersecting space of the leg length and leg orientation UCMs. It appears that the neuromuscular system only chooses to operate in this intersecting UCM space and stabilize both variables when it is absolutely critical to do so. Otherwise, the kinematic operational space appears to be maximized, presumably to allow greater adaptability to cope with other constraints or perturbations.

5.1.3 Hopping in place vs. forward hopping

From hopping in place, I see that leg length and leg orientation are performance variables whose neuromechanical importance peaks at different times in the hopping cycle. Leg length IMA shows a characteristic peak at midstance while leg orientation IMA shows a characteristic peak in mid-aerial phase (Figure 2.5). In response to task constraints that increase task difficulty, whichever variable that is affected by the change in task difficulty, either leg length or leg orientation, show an increase in average IMA (Figure 2.6 & 3.4). To test how robust these findings are for forward locomotion, I studied hopping with a forward velocity into target areas (**Chapter 4**).

Forward hopping with the large target produces the first UCM results for leg length and leg orientation stabilization in a forward bouncing gait. Since no differences in IMA are seen between the large target and no target hopping in place IMA results, even though I did not have subjects hop forward with no targets, I predict a similar result between large target and no target forward hopping. These findings provide a baseline for future studies of leg length and leg orientation stabilization in forward human bouncing gaits. Again, I see the characteristic peaks at midstance for leg length IMA and in mid-aerial phase for leg orientation (Figure 4.4). The appearance of these two peaks in every condition I tested suggests the importance of stabilizing leg length and leg orientation at their respective peaks regardless of conditions. Unique to forward hopping is a second leg length IMA peak in mid-aerial phase and leg orientation IMA being significantly less than zero during midstance (Figure 4.4). These two differences are due to the different task demands between forward and in place hopping.

As task difficulty increases with smaller targets during forward hopping, I do not observe the increases in leg orientation IMA for hopping in place. In fact, there are no changes in leg length or leg orientation IMA as target size decreases during forward hopping (Figure 4.5). Unlike hopping in place, which results in an increase in total segment angle variance with smaller targets, forward hopping does not result in an increase in variance as task difficulty increases (Figure 3.1 & 4.2). Two points about this finding need to be considered. The first relates to the increased variance in regards to stabilizing leg length or orientation during hopping in place. The second relates to the lack of change in total variance during forward hopping. The first can be explained through the results of the UCM analysis. In hopping in place, as the total segment angle variance increases, this variance was structured into stabilizing leg length through GEV and destabilizing leg orientation through NGEV (Figure 3.2). Meanwhile, the lack of increase in total segment angle variance with task difficulty in forward hopping requires no repartitioning of variance into GEV or NGEV for leg length or leg orientation stabilization (Figure 4.3). Of course, this leads to the obvious question of why total segment angle variance does not increase with target difficulty during forward hopping.

5.2 Implications of forward dynamics in accurate foot placement

The fact that I see no increase in leg length nor leg orientation IMA increases with task difficulty during forward hopping is unusual given the typical increases in IMA with task difficulty (Auyang et al. 2009; Latash et al. 2001; Reisman et al. 2002a; b; Scholz et al. 2001; Scholz and Schöner 1999; Tseng et al. 2002; Tseng et al. 2003). To evaluate the significance of this, I looked at a different performance metric that is important to precise foot placement: foot placement variability. When hopping in place, the distribution of

anterior posterior foot placement over all hop cycles does not change regardless of target size but the mediolateral distribution showed a significant decrease with smaller target sizes (Table 4.1, Figure 4.1a). In forward hopping, there was no change in the anterior posterior or the mediolateral distribution of foot placement with changes in target size (Table 4.1, Figure 4.1b). Interestingly, both the anterior posterior and mediolateral distribution of foot placement are the same as that seen during the smallest target condition for hopping in place. Subjects are able to achieve the same level of performance with no change to leg length or leg orientation IMA as task difficulty increases.

Increases in task difficulty during hopping in place shows increases in EMG activity for knee extensors and flexors while there are no changes in muscle activity during forward hopping (Figure 3.7 & 4.6). While the vasti and gastrocnemius muscles are commonly thought of as acting in a single plane, functionally, they act in multiple planes. The lower limb muscles of cats have been shown to have a significant contribution to torques along more than just one axis (Lawrence et al. 1993b). The medial and lateral gastrocnemius muscles showed significant contribution to external rotation torques about the ankle. A recent study has shown that despite the obvious contribution to sagittal plane movements, the vasti and gastrocnemius muscles of the human lower limb also have a significant role in mediolateral stabilization during human locomotion (Pandy et al. 2010). The increases in muscle activity during hopping in place could be to stabilize mediolateral foot placement as the target size decreases. During forward hopping, there are no changes in EMG activity of vasti or gastrocnemius muscles with changes in target sizes. Mediolateral foot placement performance during forward hopping does not change

with target sizes. This could be due to the passive dynamics associated with forward movement. Studies have shown that increased speed results in decreased mediolateral displacement of the center of mass (Orendurff et al. 2004). Because precise foot placement during forward locomotion is assisted by passive dynamics, there is likely to be no need to increase muscle activity or increase leg length or orientation stabilization to achieve the same level of performance in mediolateral foot placement.

5.3 Time for motor redundancy

Kinematic motor redundancy has been discussed extensively throughout this dissertation as being important to maximize the operational space such that the human body is able to adapt to perturbations and constraints. It started with an observation that the human body has more kinematic degrees of freedom than are necessary to accomplish a kinematic task in 3D space. This led to the hypothesis that there is hierarchical control of these kinematic degrees of freedom to achieve higher order performance variables, leg length and leg orientation. Because of the simplicity of the spring-mass model, I hypothesized that leg length and leg orientation would need to be stabilized throughout the entire gait cycle but this was not true. Instead, during preferred frequency hopping in place, leg length is only stabilized at midstance and leg orientation at mid aerial phase, characteristics also seen in other hopping conditions. In addition to utilizing kinematic motor redundancy to maximize the operational space, the neuromuscular system uses time as a variable in order to maximize the operational space throughout the cycle.

Albert Einstein once said, “The only reason for time is so that everything doesn’t happen at once.” I believe that the neuromuscular system uses time for just that purpose. Time is exploited such that leg length and leg orientation are not stabilized

simultaneously throughout the entire hopping cycle. Instead, both are only stabilized as they are critical to the task. Because the leg length and leg orientation UCMs are approximately orthogonal to each other (~82^{o}), most segment angle combinations that stabilize leg length would destabilize leg orientation, and vice versa. While there is an intersecting space that would simultaneously stabilize both, operating exclusively in this subspace would greatly limit the operational space, and hence adaptability, of the locomotor system. Instead, by utilizing time as a variable, leg length and leg orientation can be stabilized only as they are critical to the task thus maximizing the operational space when both leg length and leg orientation do not need to be stabilized. Leg length is important during midstance because that is when the leg is most flexed and small changes in segment angles would lead to the largest changes in leg length (**Chapter 2**). Midstance is also when peak forces are observed and shown to be stabilized (Farley et al. 1991; Yen and Chang 2009). Maintaining a specific leg length at midstance may be critical in limiting peak joint moments. Leg orientation during aerial phase is important in determining the angle of the leg at contact which in turn affects the forward velocity of the center of mass. Regardless of whether subjects are hopping in place (0 m/s) or forward, there is still a desired velocity and leg orientation stabilization during aerial phase helps achieve that velocity. When hopping in place at preferred frequencies, rather than stabilizing both leg length and leg orientation throughout the entire hopping cycle, they are stabilized by segment angle variance when they are task critical. However, that is not to say that multiple performance variables cannot both be stabilized simultaneously because as I mentioned above, there is an intersecting space where both leg length and leg orientation are stabilized.

While the neuromuscular system uses time to maximize motor redundancy by only stabilizing leg length and leg orientation when they are critical to the task, sometimes it is necessary to stabilize both. In fact, as task constraints are placed on subjects during hopping in place, there are several instances where leg length and leg orientation are stabilized simultaneously. Hopping at non-preferred frequencies results in an increase in leg length stabilization throughout the hopping cycle (Figure 2.6). As a result, both leg length and leg orientation are stabilized during aerial phase in this condition (Figure 2.5). Conversely, as the target landing area decreases during hopping in place, leg orientation stabilization increases and extended throughout the hoping cycle (Figure 3.3 and 3.4). Because of the orthogonality of the leg length and leg orientation UCMs, leg length stabilization decreases throughout most of the cycle with smaller targets. However, despite a significant decrease in leg length IMA throughout most of stance phase, both leg length and leg orientation are stabilized at midstance in the most difficult target condition (Figure 3.3). Finally, in the forward hopping condition, both leg length and leg orientation are stabilized in the aerial phase (Figure 4.4). The fact that the neuromuscular system chooses to operate in a space that limits motor redundancy during parts of the hopping cycle shows how important the stabilization of both leg length and leg orientation are to the task. For the rest of the cycle, by using time as a variable, the neuromuscular system does not have to control everything at once and therefore maintains motor redundancy when possible to cope with other constraints and perturbations.

5.4 Neural control and difficulty

The various task constraints chosen for this work were to investigate how stabilization of leg length and leg orientation changes with specific constraints that only impact one or the other. While the UCM analysis can answer the questions of "if", "when", and "to what degree" segment angle variance is structured to stabilize leg length or leg orientation, it does not address the question of "how." Studies in upper extremity tasks have shown that as the number of sensory demands increase, there are different patterns of movement-related cortical potentials (MRCPs). In a recent study, this idea has been extended to a lower extremity task of knee extension (Wheaton et al. 2007). The study found that a single task constraint (a weighted load or a target) resulted in increased cortical activity in specific areas of the cortex. Of particular interest, imposing two task constraints (a weighted load and a target) resulted in the largest increase of cortical activity. The functional interpretation of these different MRCPs and increased cortical activity was not clear to the authors.

When I consider these changes in cortical activity with my findings that structuring of segment angle variance increases with task difficulty, I can gain some insight into some of the potential physiology underlying this variance structure. Recent work suggests that the increased cortical activity associated with more complex locomoting tasks may be due to modifications of gait such as accurate foot placement (Beloozerova and Sirota 1998; 1993a; b; Drew et al. 2008). I recorded electromyography (EMG) from a subset of my subjects during the hopping in place and forward hopping tasks with different target difficulties. I chose EMG to test whether there were broad changes in the nervous system in response to different target and velocity conditions.

Because EMG is the summed output of many different contributions from the central and peripheral nervous system (CNS and PNS), I cannot conclusively say whether the changes in EMG I observe are directly related to changes in cortical activity seen in other studies. Nevertheless, during hopping in place, there is a significant increase in muscle activity for the medial gastrocnemius, lateral gastrocnemius, vastus lateralis, vastus medialis, and rectus femoris as task difficulty increases. I also see an increase in total segment angle variance with changes in difficulty during hopping in place. To contrast these findings, during forward hopping with different targets, there is no change in EMG activity or total segment angle variance. As discussed earlier, this increase in EMG activity during hopping in place is likely to minimize the mediolateral variability of foot placement. The increase in EMG activity results in a proportional increase in signal noise (Harris and Wolpert 1998) and maybe a significant source of kinematic variance. This noise can translate into variance which must be dealt with by the neuromuscular system (Faisal et al. 2008; Stein et al. 2005). In the case of hopping in place, the UCM results show that this increase in variance is structured toward stabilizing leg orientation. My results show that there is in fact purposeful structuring of segment angle variance to stabilize leg length or leg orientation at different times of the hopping cycle. I have also shown through changes in EMG activity that there are changes in either the CNS or PNS or both that result in increased EMG activity. However, the mechanisms by which this variance is structured remains unclear.

5.5 Physiological relevance of work

The neuromuscular system broadly encompasses the nervous system and the muscular system. The combined output of these two systems results in the kinematics of

locomotion. Specific examples of kinematic outputs include measures such as joint angles, segment angles, leg length, or leg orientation. Locomotion kinematic variables can be further broken into task level and local, joint level variables. As a result of separating kinematic variables into task level and local level variables, the idea of kinematic motor redundancy emerges. Study of motor control in humans is mostly limited to the outputs in the form of kinematics, kinetics, or muscle activity. Because the kinematics of gait are the summed output of the entire system, studying the different kinematic measures allows us to make inferences about how control of movement might be achieved.

By looking at just the kinematics, certain trends emerge that are far from being coincidental. In locomotion, an analysis of variance across cycles reveals that the summed total variance of leg length or leg orientation is significantly lower than the total variance of the segment angles that determine leg length and orientation. Kinematic variance provides us with a metric to test hypotheses and models of motor control. Without further analysis, it is clear that there must be some process by which the significant amount of segment angle variance is structured such that the variance of the leg length or orientation is attenuated. The UCM analysis allows us to quantify whether this variance has a purposeful structure that aligns itself with the manifold corresponding to task level variables. From my studies, the results of this analysis suggest that there is a nonrandom structure to the segment angle variance to stabilize leg length and leg orientation during human hopping. However, while the results of this analysis can explain the observations of high segment angle variance leading to reduced leg length and leg

orientation variance, it does not make any conclusions as to where or how this process is occurring in the human body.

The mechanism by which segment angle variance is structured is not clear but is likely not the result of any one mechanism. At present, it is impossible to isolate the specific mechanism that results in the structuring of segment angle variance observed through a UCM analysis. However, I can speculate on possible contributions of different physiological elements to segment coordination. Coordinating intermuscular activity is one way to achieve coordinated segment angle outputs. Muscle activity can be affected by both the central nervous system (CNS) and the peripheral nervous system (PNS). Direct control of multiple muscles from the CNS is one way to change the level of activity for different muscles simultaneously. Reflex pathways of the PNS also contribute to intermuscular coordination. Force and length feedback have a significant role in interjoint coordination (Abelew et al. 2000; Jankowska 1992; Misiaszek and Pearson 1997; Nichols and Ross 2009; Prochazka et al. 1997; Ross and Nichols 2009). During locomotion, muscles that act against gravity are modulated by heterogenic reflexes due to force feedback (Misiaszek and Pearson 1997; Ross and Nichols 2009; Wilmink and Nichols 2003). Specifically, the inhibitory heterogenic reflexes identified between ankle and knee extensors in the hindlimb of cats could serve to conserve leg orientation (Nichols and Ross 2009; Ross and Nichols 2009). For example, if there was excessive dorisflexion of the ankle, increased knee flexion would preserve a desired leg orientation value. To stabilize leg length, excitatory feedback between ankle and knee extensors or flexors would be more appropriate. An excitatory length feedback between the vasti and soleus muscles in the hindlimbs of cats would be an example of a pathway that could be

used to stabilize leg length (Wilmick and Nichols 2003). Changes in segment angles will also result in changes in muscle stretch length. The stretch reflex of ankle extensor muscles has been shown to contribute to rapid postural corrections after a perturbation. Removal of the stretch reflex through self reinnervation of the triceps surae of the cat resulted in decreased interjoint coordination during sloped walking (Abelew et al. 2000; Maas et al. 2007). Heterogenic reflexes provide possible mechanisms for intermuscular and interjoint communication to achieve segment angle coordination. Length and force feedback are not mutually exclusive of each other. Autogenic and heterogenic feedback from muscle length also plays a role in modulating muscle forces (Burkholder and Nicols 2000) and maintaining postural stability (Bunderson et al. 2007). Interneurons that receive group 1a afferents also receive inputs from group 1b (Jankowska 1992). Together, these reflexes provide a tuned network by which muscle activity can be coordinated for purposeful action. Changes in force and length of a muscle or group of muscles could be compensated for by another muscle or group such that a performance variable is still preserved.

Segment angle coordination can also be attributed to the passive mechanics of the anatomical structures. Biarticular muscles couple actions of two joints and have been shown to distribute energy across joints to compensate for perturbations (Biewener and Daley 2007; Prilutsky and Zatsiorsky 1994). Fascia also affects intermuscular activity as it has a significant force transmission effect on both agonist and antagonistic muscles (Meijer et al. 2007; Rijkelijkhuizen et al. 2007). While it was outside the scope of this dissertation to test for each of these possible mechanisms, I was able to measure muscle activity through surface electromyography to see if there are changes in muscle activity

that may be associated with likely mechanisms. Like kinematics, muscle activity recorded through electromyography is a summed output of the muscle due to inputs from CNS and PNS. This makes it difficult to conclude the cause for any changes in muscle activity. However, it does show that changes in muscle activity correlate with different tasks or changes in UCM results and this brings us closer to a physiological mechanism for how the neuromuscular system manages a redundant system to achieve stable locomotion.

5.6 Advantages of hierarchical control

A large motivation for this work comes from trying to understand how the neuromuscular system might simplify control of many degrees of freedom. Controlling a complex system with so many different elements seems like a daunting task when we consider the complex actions we are capable of. One possible control scheme, as I have proposed in this dissertation, is a hierarchical organization. Specifically, I explored the relationship between the joint level variables, segment angles, and limb level variables, leg length and leg orientation. The results of the UCM analysis support this organization by showing a nonrandom structure to the segment angle variance to stabilize leg length or leg orientation. I propose a hierarchical organization of control because I believe it "simplifies" the organization of control. At first glance, it can be counter intuitive as to why this organization is "simpler." A hierarchical organization of control actually introduces more variables into the system. For example, in regards to the variables discussed in this dissertation, without hierarchical organization only four segment angles would need to be controlled. However, with my proposed hierarchy, there are now a total of six variables (four segment angles, leg length, and leg orientation). One could argue

that hierarchical organization of control does not simplify control but in fact makes it more complex. So it is important to discuss what aspects of locomotor control are simplified through hierarchical organization.

The main advantage of hierarchical control is that it provides modular control of different elements of the neuromuscular system. The advantage of modular control becomes apparent when we consider a response to perturbations. To discuss this, let's first consider the alternative to hierarchical control where all local variables are directly controlled by higher centers and there are no additional organizational levels. In this organization, perturbations to the system would require a new set of descending commands to all local variables. In short, to respond to even minor perturbations, all local variables would have to be modified to compensate for the perturbation. It is important to note that this control structure most likely would still operate within a set of goal equivalent solution space. This solution space would be comprised of all elements of the system though. Computationally, this organization increases the real-time demand on higher centers, as new descending commands will have to be issued instantaneously to all local variables every time the system is perturbed. In order to continue operating within the goal equivalent solution space with simultaneous or sequential perturbations, the system would require constant retuning of the entire system. So while this organization has a lower total number of variables controlled in the entire system, any changes to the system would require adjustments to all local variables. This increased computational demand can be avoided by organizing control in a hierarchical structure that allows for modular control at each level. Modular control allows for localized responses to

perturbations in specific areas of the hierarchy as opposed to a global response of the whole system.

Despite an increase in the overall number of variables in the control system, hierarchical organization provides for a modular control scheme. Each element within a level of the hierarchy can be thought of as having its own set of goal equivalent solution space defined only by elements in a lower level of the hierarchy that have significant contribution. Another way to consider this is that each element in a level is a "mode" or "synergy" that is a function of certain lower level variables. Examples of this in this work would be leg length or leg orientation as a function of segment angles (Figure 4.8). Compensation to perturbations can be isolated to the synergies that are affected, such as leg length or leg orientation, rather than adjustments to all variables in the system. This allows for modular control of different elements in the system such that only the elements that are affected by a perturbation are adjusted as opposed to the retuning of the entire system.

In my proposed hierarchy of control, I have described the lowest level as segment angles and how these variables are organized to stabilize higher order performance variables. While it was not discussed or explored, it is important to note that individual segment angles can also be stabilized. It is likely that each segment angle is stabilized through its own set of local variables. In the case of joint torques, it has been shown that when hopping at higher frequencies, total limb force stabilization relies almost entirely on the ankle torque (Yen and Chang 2010), which is controlled by multiple muscles that cross the ankle joint. There is most likely feedback within each hierarchical level as well as between hierarchical levels. So while a hierarchical control of variables introduces a

more complex organization and more total variables, the result is an organization that allows for modular control of only task critical variables instead of all elements of the system whenever the system is perturbed.

5.7 Limitations and future work

This dissertation work explores a two level hierarchical control structure that relates joint level segment angles to task level performance variables leg length and leg orientation during a human hopping task. This was done using a UCM analysis. The UCM method can determine whether, on average, there is a purposeful, nonrandom structure to the cycle to cycle segment angle variance to minimize the variance of leg length or leg orientation. It does not, however, answer the question of how this is accomplished. Though I have speculated into potential physiological mechanisms, future work using other methods and experimental models should aim to elucidate these mechanisms.

The UCM method is capable of determining whether there is a nonrandom structure to the small cycle to cycle segment angle variance. In other words, this method is only appropriate for analyzing cyclical, repeatable cycle to cycle tasks such as the hopping tasks used in this dissertation. Future studies that investigate how the locomotor system compensates to sudden, discrete perturbations that result in an acute, single cycle deviation should be cautious of using this method. A major limitation of this analysis is that we must have some knowledge of what the desired value for a performance variable is. For this dissertation work, I use a reference posture, defined as the mean value of performance variable at a particular point in time across all the cycles, as the desired

performance variable value. A sudden perturbation would cause large deviations to the mean reference posture and therefore would affect the results.

Throughout this work, I have discussed the purposeful structuring of segment angle variance into GEV to minimize the variance of leg length or leg orientation. However, that is not to say that the only purpose of structuring variance is to minimize leg length and orientation variance. Segment angle variance can also be purposefully structured into NGEV. Because the NGEV component of lower level variables, such as segment angles, gets translated up the hierarchy, the purposeful structuring of variance into NGEV may be to stabilize higher order variables. While this work describes two levels of a hierarchy, it is likely that there exist higher (and lower) order variables relative to the ones shown in this work. I present some evidence in Chapter 4 that step length may be a higher order performance variable than leg length or leg orientation (Figure 4.8). The NGEV components that directly increased variability of leg length and leg orientation could be further structured to stabilize higher-level variables, such as step length. Future work should explore whether there are in fact higher (or lower) order performance variables that can be stabilized. Understanding higher order performance variables may give insight into potential advancements in locomotor controllers and rehabilitation of patients that have deficits in lower level variables.

The locomotor gait studied in this work was human hopping. While, human hopping was chosen because it is the simplest form of a human bouncing gait, human running is a much more common form of bouncing gait. It is debatable how similar control of human hopping is compared to that of human running. However, my results from forward hopping shows that there are definitely consistent leg length and leg

orientation control characteristics with hopping in place which suggest translation of this work to human running. Future work should expand on this with the goal of studying human running and eventually human walking.

Kinematic motor redundancy has been discussed as useful in allowing for a seemingly infinite number of segment angle combinations for a given performance variable value. However, combinations at the extremes of the solution space do not seem to be used often, if at all. The limits of the solution space that the neuromuscular system chooses to operate in may coincide with a set of optimal combinations that satisfy some other as yet unidentified conditions. The conditions around which these optimal combinations depend should be investigated and may give insight into higher order performance variables as well. One possible experiment is to limit the segment angle solution space with a physical constraint and observe whether there are changes in hypothesized higher order performance variables.

This dissertation only begins to explore the hierarchy of performance variables that are critical to human bouncing gaits and locomotion in general. A better understanding of task critical performance variables, their sensitivity to different task constraints, and their relationship with different joint level variables will be invaluable to our understanding of normal locomotion and motor control in general. Also, discovery of such fundamental principles can be helpful in developing new gait rehabilitation and therapy of patients with neuromuscular deficits. This knowledge may also be useful in creating a new metric by which to clinically evaluate patients in physical rehabilitation.

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Vita

Arick Gin-Yu Auyang was born in Frankfurt Germany. He moved to Hong Kong before coming to the United States in 1988 where he attended UMS-Wright in Mobile, Alabama until he graduated in the Class of 2000. In 2003, he received a Bachelor of Science in Biology at Emory University in Atlanta, Georgia. After graduation, he worked as a research assistant for Dr. Richard Nichols at Emory University on a project with Dr. Young-Hui Chang. In 2005, began his graduate work at the Georgia Institute of Technology, pursuing a doctorate in the first class of the new School of Applied Physiology. He hopes his work will insight into the fundamentals of human locomotion to better assist with the rehabilitation of persons with gait pathologies. Outside of work, he enjoys outdoor activities, photography, and just spending time with friends and family.